GROWTH AND MATURITY OF THE PACIFIC RAZOR CLAM, *SILIQUA PATULA,* IN

EASTERN COOK INLET, ALASKA

By

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GROWTH AND MATURITY OF THE PACIFIC RAZOR CLAM IN EASTERN COOK INLET, ALASKA

A

THESIS

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Abstract

In Alaska, the only road-accessible fishery for the Pacific razor clam, *Siliqua patula*, is located in eastern Cook Inlet, and has been monitored by the Alaska Department of Fish & Game (ADF&G) since 1964. In recent years, a shift has been observed in size, age, and number of clam cohorts in this region, yet little is known about the early life history of razor clams in this region. This study aimed to provide information on length and age at maturity, growth rates, and spawn timing at two beaches in eastern Cook Inlet, Ninilchik and Clam Gulch, in 2009 and 2010. At Clam Gulch, only 20% of the sampled population was reproductive, compared with 83% at Ninilchik. At Ninilchik, clams were reproductive at a smaller size and younger age ($p<0.05$) than previously documented. The Ninilchik clams grew faster and had a larger size at age ($p<0.05$) than at Clam Gulch. A body condition index of clams from Clam Gulch was consistently 50% lower than at Ninilchik. Despite the relative proximity (25 km) of these locations, it is possible that environmental conditions may be different, resulting in differences in growth and reproductive output. This information is of special interest to fisheries managers as they address recent declines in the eastern Cook Inlet razor clam population and provides a benchmark for future management decisions.

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Dedication

This thesis is dedicated to my children, Matthew and Talya Encelewski. Their patience, love, and understanding enabled the many hours of research, contemplation, and writing necessary to complete this project.

> "*At the mouth of Cook's River, lat 59 degrees, 61', are many species of shell-fish, most of them, I presume, nondescript. For a repast, our men preferred a large species of the Solen genus, which they got in quantity, and were easily discovered by their spouting up water as the men walked over the sands which they inhabited: as I suppose it to be a new kind I have given a figure in the annexed plate. 'Tis a thin, brittle shell, smooth within and without; one valve is furnished with two front and two lateral teeth; the other has one front and one side tooth, which slip in between the others in the opposite valve: from the teeth in each valve proceeds a strong rib, which extends to above the half way across the shell and gradually loses itself towards the edge, which is smooth and sharp. The color of the outside is white, circularly, but faintly, zoned with violet, and is covered with a smooth yellowish-brown epidermis, which appears darkest where the zones are: the inside is white, slightly zoned, and tinted with violet and pink. The animal, as in all species of this genus, protrudes beyond the edge of the shell very much, and is exceeding good food*."
>
> -Captain George Dixon, “A Voyage Around the World, but More Particularly to the North-West Coast of America, 1789”

Introduction[1]

There has long been a need for more information about Pacific razor clam (*Siliqua patula*) populations in eastern Cook Inlet. In the mid-2000s, the Alaska Department of Fish and Game (ADF&G) observed that all clams age 7 and older had disappeared from a large section of eastern Cook Inlet beaches, followed by years of slower than average growth (Szarzi and Hansen 2009). Furthermore, the ADF&G has observed that there are fewer age classes present on eastern Cook Inlet beaches than in years past, and that overall abundance of razor clams is in decline (M.D. Booz, ADF&G, personal communication). These observations were the incentive for the present study on reproductive ecology and age structure of Pacific razor clams in eastern Cook Inlet. This study was conducted in 2009 and 2010 to gather information on spawn timing, age at maturity, and growth of razor clams in eastern Cook Inlet. Data collected during this study were compared with historical length and age data provided by the ADF&G. Additionally, a goal of this study was to validate the current aging methodology used by the ADF&G. The data collected here will enhance ADF&G's knowledge of Pacific razor clam early life history in eastern Cook Inlet, and aid in the sustainable management of the species.

Biology and ecology of razor clams

The Pacific razor clam is a soft-shelled bivalve found on sandy, exposed beaches along the west coast of North America from Pismo, California to the Bering Sea in Alaska (Weymouth and McMillin 1930, Leclair and Phelps 1994). Razor clams can burrow into the sediment to a depth of about 25 cm and are found from the intertidal zone to approximately 18 m water depth

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[1] Thesis is formatted according to guidelines of the journal *Transactions of The American Fisheries Society*

(Bourne 1969, Jones et al. 1998). They play an important ecological role in these often low-diversity environments by providing hard structure within the homogeneous sandy substrate (Gutierrez and Iribarne 1999). In addition, razor clams play a role in pelagic-benthic coupling by feeding on local phytoplankton sources, thus transferring a substantial amount of the primary production in the water column to benthic organisms (Lewin et al. 1979a, 1979b; Dame et al. 2001). The clams' filtration activity also helps to reduce turbidity and fertilize benthic habitats through biodeposition, and thus plays a vital role in ammonium re-mineralization by influencing nutrient cycling in the local environment (Dumbauld et al. 2009). Similar to some other bivalve filter feeders, razor clams are prone to accumulating marine toxins from phytoplankton, such as domoic acid, which is harmful to human and other trophic level consumers (Horner et al. 1993, Wekell et al. 1994). Natural predators on razor clams include brown bears (*Ursus arctos*), oystercatchers (*Haematopus bachmani*), sea otters (*Enhydra lutris*), and various eider ducks (*Somateria* spp.), gulls (Family: Laridae), crabs, and some fish species (Johnson 1982, Bishop and Powers 2003, Smith and Partridge 2004, Freudendahl et al. 2010).

Growth rate of the Pacific razor clam are dependent on environmental parameters, such as food availability and seawater temperature (Nickerson 1975, Lassuy and Simons 1989). Cooler temperatures lead to slower growth rates among Alaskan populations relative to stocks found in the southern reaches of their geographic distribution (Weymouth et al. 1925). However, maximum length is smaller for southern populations (Weymouth and McMillin 1930, Taylor 1959, D. Nelson, ADF&G, unpublished data). For example, more southern razor clams generally reach a maximum age of five years and about 120 mm in length in California and a maximum of six years and about 100 mm in Washington (D. Ayres, Washington Department of Fish & Game [WDF&G], personal communication). In comparison, they can reach 12 to 13 years of age and about 175 mm in length in Alaska (Nickerson 1975). On occasion, razor clams as old as 19 years of age have been recorded in Alaska (Weymouth et al. 1925, Nickerson 1975).

Razor clams have separate sexes, and reproduction starts with slow gonad development over the winter that increases in early spring (Weymouth et al. 1925, Bourne and Quayle 1970). Prior to spawning in the spring, gonads increase in weight, and ripening of the gonad tissue can be observed microscopically (Helm and Bourne 2004). Spawning occurs annually and is most likely triggered by an increase in seawater temperature, with the minimum temperature for spawning in the coastal waters of Washington occurring at approximately 13ºC (Weymouth et al. 1925, Nickerson 1975, Breese and Robinson 1981, Lassuy and Simons 1989). In Alaska, spawning is thought to occur when seawater temperatures rise to just above 8ºC (Nickerson 1975). In the Pacific Northwest, the required temperature and subsequent spawning occurs between May and September, and spawning takes place progressively later with increasing latitude (Lassuy and Simons 1989). In Alaska, peak spawning typically occurs in late July and early August (McMillin 1924, Lassuy and Simons, 1989). When gonad maturity and threshold temperatures are reached, razor clams release gametes into the water column with females producing an estimated 300,000 to more than 100 million eggs per spawning event (McMillin 1924, Nickerson 1975, Lassuy and Simons 1989). Eggs are externally fertilized, after which a planktonic trochophore larva develops (Nickerson 1975, Lassuy and Simons 1989). Within approximately 10 days, the free-swimming veliger stage forms (McMillin 1924, Brinks 2001). Larvae drift in the water currents for an estimated 8 to 10 weeks before developing into a sedentary juvenile. By the time of settlement, razor clams may be widely distributed from the point of origin by currents and tides (Jones et. al 1998).

Sexual maturity in razor clams is related more to size (length) than age (Bourne and Quayle 1970, Nickerson 1975). In Alaska, razor clams are thought to first mature during their third or fourth growing season, or when they reach approximately 100 mm in shell length (Nickerson 1975, D. Nelson, ADF&G, unpublished data). However, spawning has been observed in eastern Cook Inlet, Alaska, in some specimens as small as 86 mm (McMullen 1967). Conversely, some individuals greater than 100 mm in length may not yet have reached reproductive maturity (D. Nelson, ADF&G, unpublished data). At Ninilchik Beach, lower Cook Inlet, razor clams generally reach 100 mm by the formation of the fourth annulus, while 25 km to the north at Clam Gulch Beach, 100 mm in length is reached by the formation of the fifth annulus (D. Nelson, ADF&G, unpublished data). These data suggest that maturity may occur one year earlier at Ninilchik than at Clam Gulch. Although the cause of this small-scale difference is unknown, site-specific environmental factors, such as seawater temperature, food availability, and ocean currents, may be responsible (Seed 1980).

Age assessment of clam populations

Estimations of growth rate and age structure are basic management tools used to track year classes as they age, and to measure annual growth. In clams, these measures depend on the accurate identification of annular shell growth rings (Richardson et al. 2004). Other aging methods such as shell sectioning (Neves and Moyer 1988), acetate peels (Ropes 1984, Leontarakis and Richardson 2005), electron imaging (Karney et al. 2011), and stable oxygen isotope analysis (Richardson et al. 2004) are cost- and labor-intensive, and often impractical when processing large numbers of samples.

Counting annular shell rings is a common method to directly assess the chronological age of bivalves (Quayle and Bourne 1972, Sukhotin and Flyachinskaya 2009). Growth increments of bivalve shells appear as alternating zones of opaque and translucent material (Campbell et al. 2009). These zones result from varying proportions of conchiolin and aragonite within the shell material (Rhoades and Lutz 1980, Campbell et al. 2009). During summer months, warm water temperatures and abundant food supply lead to a period of higher metabolism and fast growth, which is marked by a light-colored band with greater amounts of aragonite (Campbell et al. 2009). In winter months, colder temperatures lead to lower metabolism and a decline in food, resulting in the cessation of growth marked by a dark, narrow band in the shell composed of proportionately less aragonite (Campbell et al. 2009). These dark bands are used as a marker of annual growth (Neves and Moyer 1988, Lassuy and Simons 1989, Campbell et al. 2009).

The annular ring aging technique can be confounded when the first annulus (year mark) is difficult to discern, particularly in older specimens (Neves and Moyer 1988). Because the first annulus is formed when the shell is still very thin, it may be difficult to detect as the clam ages and the shell thickens (Bourne and Quayle 1970). The clarity of subsequent annular rings can depend on several factors, including the contrast in seawater temperature during winter and summer growth periods, food availability, seasonal changes in dissolved oxygen, and salinity (Tegelberg 1964, Bourne and Quayle 1970). A true annulus can be traced from the umbo to the shell margin (Neves and Moyer 1988), while pseudoannuli or “false” annuli are characterized as an incomplete growth line occurring in thin shell sections (Neves and Moyer 1988). These false annuli may result from stressors, such as predation (Richardson et al. 1980), spending prolonged time periods exposed during extreme low tides (McMullen 1967, Campbell et al. 2009), or other disturbance events. In horse clams (*Tresus nuttallii*), “false” annuli are most detectable during the first three years (Campbell et al. 2009), but have also been identified in older razor clam individuals in Alaskan waters (M.D. Booz, ADF&G, personal communication).

In addition to growth rate and age structure, morphometric condition indices (CI) can be used to indicate the energy balance of a tissue or an animal (Lucas and Beninger 1985, Brown and Hartwick 1988). Morphometric CIs express the proportion of dry soft tissue weight to shell weight. A low or declining body mass may indicate that a major biological effort has been expended, either as maintenance energy under poor environmental conditions or disease, or in the production and release of gametes during spawning events (Lucas and Beninger 1985, Norrko et al. 2005). It should be noted that morphometric CIs do not account for variations in internal shell cavity capacity (Mann 1978) and do not represent an index of nutritional status (Crosby and Gale 1990). However, morphometric indices have been widely used as a crude indicator of energy balance because they are easily standardized and have greater universal application than many other indices (Filgueira et al. 2013).

Razor clam management in Alaska

In Alaska, razor clams are a commercial and recreational shellfish resource managed by the ADF&G. Razor clams are found along the entire coast from southeast Alaska to the Bering Sea, and are concentrated in four main areas: Swikshak on the Alaska Peninsula, Cordova in Prince William Sound, Polly Creek in western Cook Inlet, and along the 80-km stretch between the Kasilof and Anchor Rivers in eastern Cook Inlet (Nickerson 1975; Figure 1). The populations in eastern Cook Inlet comprise the only road-accessible recreational (sport) razor clam fishery in Alaska.

Following the 1964 earthquake, the ADF&G implemented a study of the eastern Cook Inlet razor clam populations (D. Nelson, ADF&G, unpublished data). Aerial surveys began in 1966 to estimate recreational razor clam digging effort in eastern Cook Inlet, with reliable data available since 1971 (Szarzi 1991). The ADF&G data indicate that annual harvest from 1977 to 2009 averaged 900,000 clams in eastern Cook Inlet (Szarzi and Hansen 2009). The majority of razor clams harvested in eastern Cook Inlet are taken at Ninilchik and Clam Gulch beaches. Ninilchik Beach has been consistently more popular than Clam Gulch since 1986 and, since 2006, more than 60% of the area harvest has been taken from Ninilchik Beach (Kerkvliet and Booz 2013), while approximately 20% of the harvest occurred in the Clam Gulch area (Szarzi and Hansen 2009).

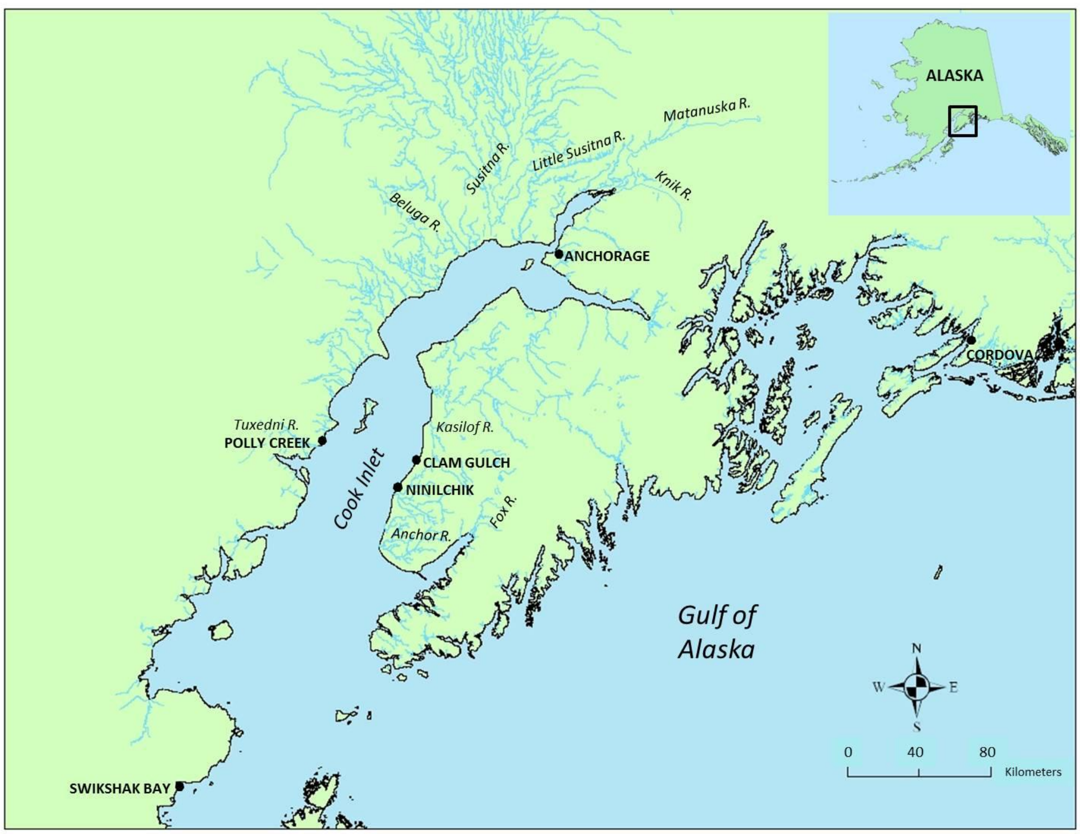

Figure 1. Locations of Pacific razor clam concentrations in Alaska (see references in text). Major cities are included on the map for reference.

In 2005, the ADF&G observed an unusual disappearance of all razor clams age 7 and older from a large section of the eastern Cook Inlet beaches, including Clam Gulch, followed by slower growth of the remaining animals than had previously been observed (Szarzi and Hansen 2009). The ADF&G also observed that the average size and age of clams harvested in eastern Cook Inlet began to shift, and that there were fewer age classes present on the beach than in the past (M.D. Booz, ADF&G, personal communication). In 2008, abundance at Clam Gulch was estimated to be 3.6 million clams, down from previous estimates ranging from 7.2 to 9.1 million clams in 1988 and 1999, respectively (Szarzi and Hansen 2009). Clam abundance in Ninilchik in 2013 was estimated at just 79,000 clams (ADF&G, unpublished data), down from 4.4 million in 2003 and 1.7 million in 2011 (Szarzi and Hansen 2009, ADF&G, unpublished data).

Prior to spring 2013, state regulations allowed diggers to take the first 60 clams dug per day, year round, at any location in the eastern Cook Inlet fishery. The 60 clam per day limit had been in effect since 1962, except from 2000 to spring 2003, when the daily bag limit was reduced to 45 clams because of concerns by local residents (Szarzi and Hansen 2009). In May 2013, an emergency order reduced the daily bag limit to 25 clams. However, despite these management implementations on bag limits, the abundance of clams has been steadily declining.

The recreational harvest pressure and observed changes in population structure and concentrations of Pacific razor clams in eastern Cook Inlet over the last decade make this clam population of particular interest to resource managers, thereby warranting careful monitoring by the ADF&G. The ongoing monitoring effort indicates that razor clam abundance, growth rates, and age structure may differ among individual locations in eastern Cook Inlet, despite their close proximity. Previous studies of eastern Cook Inlet razor clam populations have investigated their abundance and distribution (Szarzi 1991), but fisheries managers have very little information about the early life history, current age structure, and growth of razor clams in eastern Cook Inlet.

The goal of this study was to provide information on length and age at maturity, as well as spawn timing, at two popular recreational razor clam digging beaches in eastern Cook Inlet – Ninilchik and Clam Gulch. Specifically, this study aimed to identify the timing and duration of razor clam spawning in eastern Cook Inlet, as well as the clam size and age at which spawning occurs. As secondary objectives, this study aimed to assess growth rates at the two study sites, including a comparison with historical growth rates from ADF&G monitoring data. Finally, this study attempted to validate the current razor clam aging techniques employed by the ADF&G. These data will aid in the sustainable management of razor clams by providing important information about the early life history of razor clams in eastern Cook Inlet.

Methods

Study area

Cook Inlet is a large, elongated body of water in southcentral Alaska, extending from the Gulf of Alaska to Anchorage (Figure 1). The inlet is approximately 270 km in length, and ranges from 19 to 86 km in width. Cook Inlet experiences maximum tidal ranges of ~8 m in the lower inlet to ~11 m in the upper inlet near Anchorage. The main tributaries that supply freshwater and suspended sediments to the inlet are the Beluga, Knik, Little Susitna, Matanuska, and Susitna rivers. These drainages supply approximately 70 to 80% of the freshwater inputs and 75 to 90% of the suspended sediment input to upper Cook Inlet (Rosenberg and Hood 1967, Feulner 1971, Feely and Massoth 1982). The lower Cook Inlet area receives suspended sediment from smaller rivers, including the Kenai, Kasilof, Ninilchik, Anchor, and Fox rivers on the east side of the inlet and the McArthur, Big, Drift, and Tuxedni rivers on the west side of the inlet (Feely and Massoth 1982). Inflowing Gulf of Alaska water, enriched with particles of marine origin, flows northward along the eastern coast of Cook Inlet until it reaches the area near Ninilchik, where it mixes with outflowing, brackish water on the western side of the inlet (Feely et al. 1980). The northward-flowing, non-tidal circulation in eastern Cook Inlet is mostly oceanic in character, while the southward-flowing, western Cook Inlet waters are freshwater influenced and carry more terrigenous particles (Feely et al. 1980, S. Okkonen, University of Alaska Fairbanks [UAF], personal communication). Within this non-tidal circulation system, Ninilchik is located about 25 km upstream (south) of Clam Gulch, and may have coastal waters that are more oceanic in character than at Clam Gulch, where more mixing with brackish water occurs (S. Okkonen, UAF, personal communication).

Although the 80-km coastline on the east side of Cook Inlet is one continuous beach containing razor clams, the ADF&G divided the eastern Cook Inlet area into six razor clam study sites, based on slight differences in beach morphology, razor clam population characteristics, and recreational clam harvest distribution (Szarzi et al. 2010). Two of these study sites, Ninilchik (60°3'32.52"N, 151°39'31.65"W) and Clam Gulch (60°14'43.23"N, 151°23'51.71"W, approximately 25 km north of Ninilchik) are of particular interest to the ADF&G due to their popularity among recreational clam diggers. During this study, samples were collected along 1.2-km stretches at the north end of each site (Ninilchik and Clam Gulch; Figure 2) established by the ADF&G monitoring program. Both areas are typical razor clam habitat, with flat to gently sloping beaches exposed to strong surf action. The sediments in these areas are composed mainly of medium- to fine-grained sands, mixed with occasional silt and clay sediments (Feely and Massoth 1982, Szarzi 1991).

Sampling

In 2009 and 2010, adult razor clams were collected at Ninilchik and Clam Gulch from June through October and April through October, respectively, along the designated beach areas. During both field seasons, at least 100 adult clams were haphazardly collected at each beach every month between the +0.3 m and -1.2 m tidal elevations, depending on the tidal height at the time of collection. Typically, clams were sampled to about 30 to 50 cm depth at locations where a small hole in the sediment (called a “show”) indicated the presence of a clam.

Figure 2. Study sites at Ninilchik (top) and Clam Gulch (bottom) beaches.

Gonad maturity

Clams from 2010 collections were sexed and reproductive status was determined for each individual. A lateral incision was made into the digger foot of each female, and a fresh gonad tissue smear was prepared on a microscope slide. Each smear was examined at 10x and 40x magnification using a compound microscope (Ward's Model M3C). Female gonad maturation stage was quantified using an established qualitative index (J. Deibert, Washington Department of Fish and Game, personal communication; Table 1, Figure 3), and the reproductive status of female razor clams at the two study beaches was compared. Mature male clams were identified based on the presence of gonad material, but maturity stages were not indexed. The lack of gonad development in immature clams did not allow gender to be distinguished in those clams.

Length and age at maturity

Soft tissue was removed from shells and set aside for weight determination to calculate a morphometric condition index (see below). Shell length was measured with vernier calipers to the nearest 0.01 mm in both study years. Shells were air-dried overnight and each shell pair was assigned a unique identifier. Shells were then soaked in a 50:50 bleach:water solution for approximately 1 h to remove the periostracum and enhance the visibility of annular rings. Shells were again air-dried overnight, and the edges were covered with clear packing tape to prevent breakage. Clam shells were aged by counting the annular rings (visible as dark rings extending to the shell margin when held against a high-intensity light) from the innermost ring closest to the umbo to the outermost ring closest to the shell margin (Figure 4). Each complete annulus was

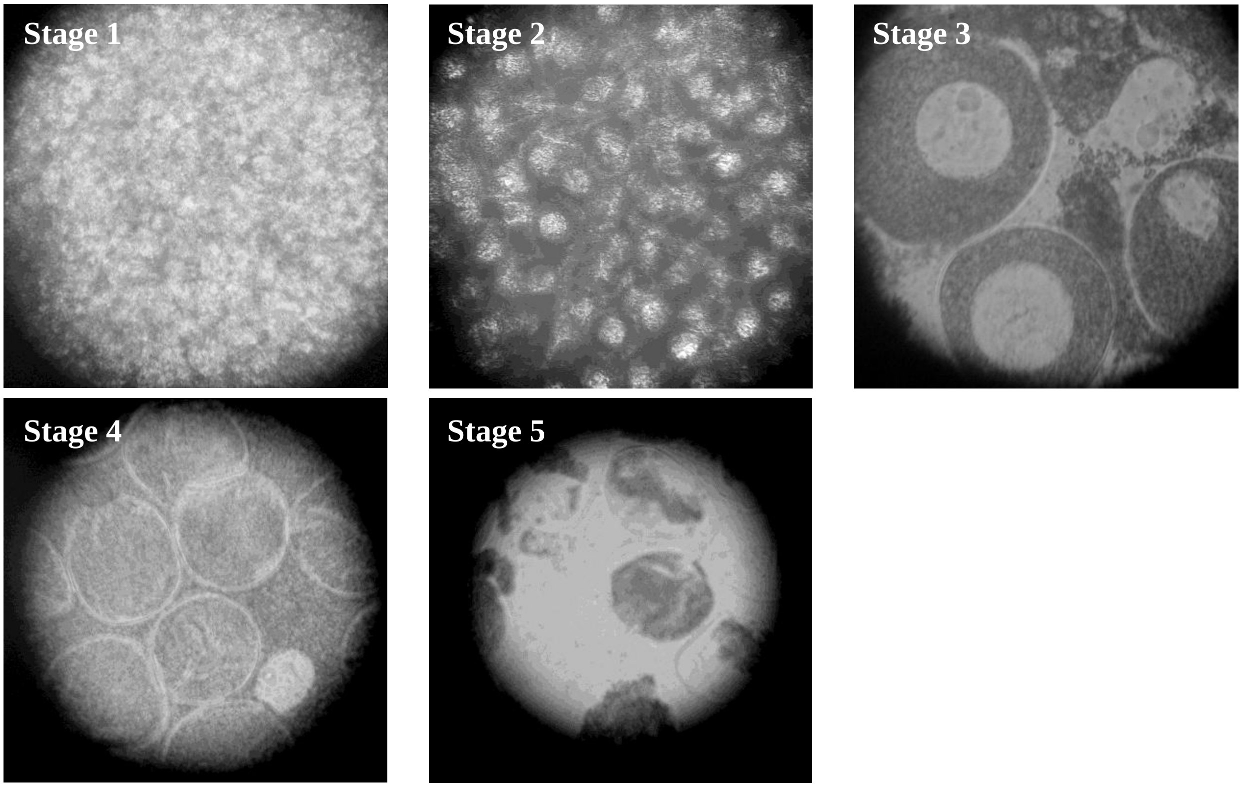

Figure 3. Reproductive development stages in female Pacific razor clam gonads. Stage 1 – Undeveloped/indeterminate sex, Stage 2 – Developing reproductive follicle, Stage 3 – Mature reproductive follicle, Stage 4 – Post-spawning reproductive follicle, Stage 5 – Reabsorbing follicle (scoring after J. Deibert, Washington Department of Fish and Game (Table 1), photos by J. McKellar).

Table 1. Reproductive stages of female razor clams.

Stage	Characteristics
1	Undeveloped/indeterminate sex – Gonadal follicles are absent and sex determination is not possible. Stage 1 clams are not reproductive
2	Developing reproductive follicle – Follicles are filled with oocytes
3	Mature reproductive follicle – Follicles are very large and occupy almost the entire portion of the digger foot and digestive tract
4	Post-spawning reproductive follicle – Follicles have contracted and occupy less gonad volume than in mature individuals; very few oogonia present
5	Reabsorbing follicle – Follicle walls are disrupted and broken down

considered to represent one full year of growth. Shells were also examined for the presence of "false" annuli (rings that do not reach the shell margin). Clams were aged using the direct aging method by counting annuli from the umbo to the shell margin, which is currently used by the ADF&G, and described by D. Nelson (ADF&G, unpublished).

Growth

A von Bertalanffy growth model (von Bertalanffy 1938) was used to estimate predicted mean maximum length (mm) at age (in years) from the number of annuli and shell length:

$$L_\infty = L_t\,(1-e^{K(t-t_0)}),$$

where L_∞ is the predicted maximum shell length, L_t is the actual length at time t, K is the Brody growth coefficient, and t_0 is the theoretical time at which an organism has zero length. The von Bertalanffy growth model assumes that the growth rate is a constant, which fails to hold for many animals whose growth rate varies seasonally (Cloern and Nichols 1978); however, the von Bertalanffy model has been widely used in other razor clam studies (e.g., Hirschorn 1962, Fahy and Gaffney 2001).

Phi-prime (ϕ; Pauly and Munro 1984), a measure of growth performance often used in fish and shellfish (Brey 2001), is based on the von Bertalanffy growth equation and was used to compare the razor clam growth parameters obtained in this study with those from historical populations at Ninilchik and Clam Gulch:

$$\phi = \log K + 2 \log L_\infty$$

The overall growth performance index (P), which represents growth rate at the point of inflection on the size-growth curve (Pauly 1979), is another measure of growth comparison among studies and was used to calculate a relative comparison of razor clam growth among locations on the west coast of North America:

$$P = \log (K[L_\infty]^3)$$

For both phi-prime (ϕ) and overall growth performance (P) estimations, the variables K and L_∞ are defined as for the von Bertalanffy equation.

Morphometric condition index

During the 2010 field season, shells were weighed and soft tissue was dried at 60°C for 24-36 h (Fisher Scientific 516G drying oven). All clams and shells were weighed to the nearest 0.01 g using an A&D HL-400 digital scale. These measurements were used to calculate a morphometric condition index (CI; Lucas and Beninger 1985, Crosby and Gale 1990, Marsden 2004) at Clam Gulch and Ninilchik:

$$CI = \frac{\text{Dry Tissue Weight}}{\text{Dry Shell Weight}} \times 100$$

Detection of age-1 annulus

Juvenile razor clams were collected at each beach from sediment samples taken monthly between May and October 2009 and between May and July 2010, as well as opportunistically during the previously described adult collection events. Rebar stakes were used to permanently mark the -0.3 m, -0.6 m, -0.9 m, and -1.2 m elevations, along which sediment samples were taken. Sampling each month commenced at a different randomly chosen distance from each elevation marker. A 10-cm diameter x 25-cm depth (4,600 cm^3 volume) PVC core (“clam gun”) was used to collect ten replicate sediment samples 15 m apart along each elevation.

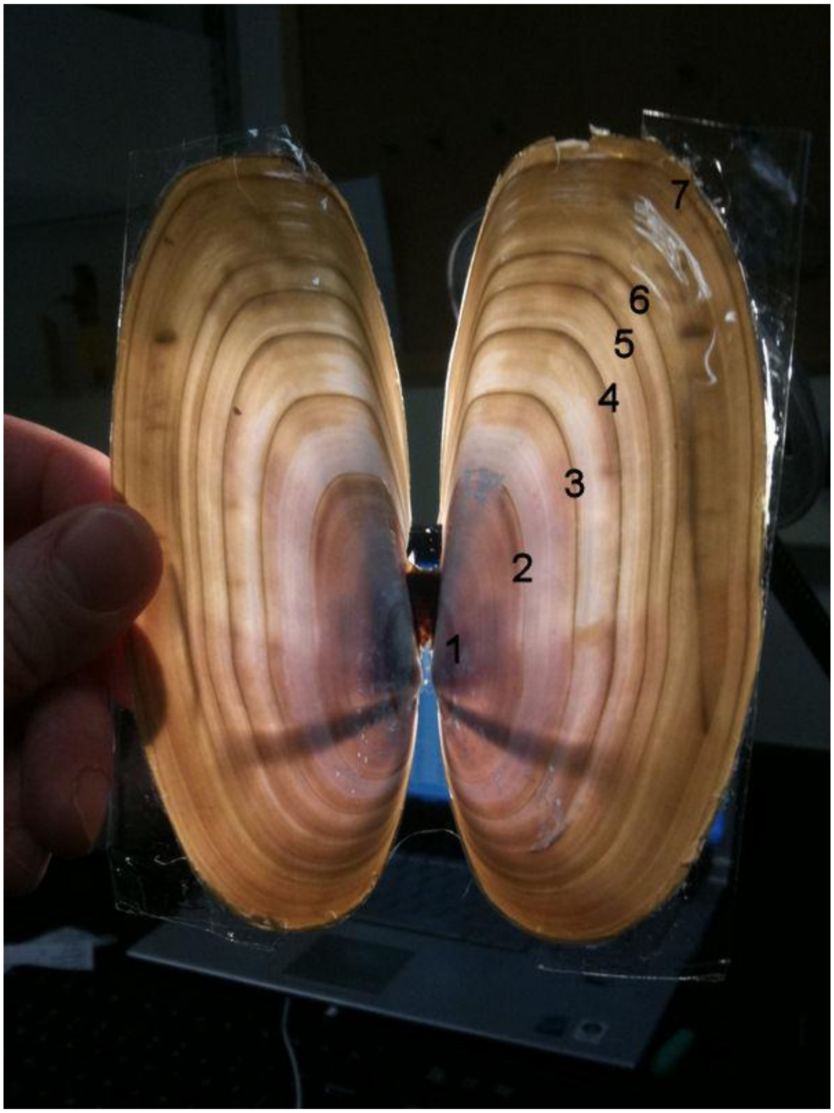

Figure 4. Pacific razor clam shell with periostracum removed to enhance visibility of annular rings. This individual was estimated to be 7 years old.

In 2009, sediment samples were washed through a 1-mm mesh sieve. In 2010, sediments were washed through 425-μm and 250-μm nested mesh sieves to ensure that juveniles smaller than 1 mm would be detected. All clams retained by the mesh were dried, measured along their longest axis and examined for the presence of annular rings. In addition, high abundance of a young age class (2007 age class) in the Ninilchik area provided an opportunity to investigate early razor clam growth and the persistence of the first annulus over time during this study.

Alaska Department of Fish & Game (ADF&G) database

Historical monitoring data for razor clam size and age from Ninilchik (1994-2008) and Clam Gulch (2000-2008) were compared with data collected for those sites during the present study (2009-2010). These data were used in comparisons of length-frequency distributions, age-frequency distributions, and growth curves. These historical data were obtained from a comprehensive ADF&G database for Pacific razor clams in eastern Cook Inlet (M.D. Booz, ADF&G, personal communication).

Temperature monitoring

Because temperature may affect clam growth, maturation and spawn timing, water and substrate temperatures were monitored continuously at Ninilchik and Clam Gulch from June 2009 to December 2010. Onset Tidbit V2 UTBI-001 water temperature data loggers with temperature range of -20 to +30° C (Onset Computers) were deployed at both sites. A 1.8-m rebar stake was buried 1.5 m deep in the substrate at the -0.3 m elevation stratum. Loggers were housed in PVC containers with predrilled holes to protect the integrity of the loggers, but allow water movement. The PVC housing was attached to the rebar stake using wire and an automotive hose clamp. At each beach, one logger was attached just above the substrate surface to record bottom water temperature (°C). The second logger was attached approximately 0.3 m below the surface to measure substrate temperature. In 2010, two additional data loggers, one at each depth, were added at each site to increase data reliability and eliminate data loss in the event of equipment failure. Loggers were programmed to record temperatures at 30- to 60-min intervals, and downloaded approximately bi-monthly, except during winter months, until December 2010.

Statistical analyses

A chi-square test was used to determine whether there was a significant difference in age distribution between Ninilchik and Clam Gulch and to compare the historical age distributions at each site with those determined in the present study. Independent t-tests were used to compare length-frequency distributions, condition indices, and average monthly seawater and substrate temperatures between sites. Growth performance values were tested for normality and a one-way ANOVA was used to compare values (ϕ and P) from Ninilchik and Clam Gulch. Statistical analyses were completed using the SPSS software package (Version 21), and significance level was set at $\alpha=0.05$ for all analyses.

Results

Razor clam spawning time in eastern Cook Inlet

Clams at Ninilchik (Figure 5 A) and Clam Gulch (Figure 5 B) were reproductive between May and September 2010. Mature females were still found in August at Ninilchik, but not at Clam Gulch. By September, all clams at both beaches were in the post-spawning (reabsorbing) phase (Stage 5).

Reproductive status in relation to clam length and age

The length-frequency distributions of reproductive and non-reproductive razor clams were similar at Ninilchik and Clam Gulch in 2010. At Ninilchik, reproductive clams ranged in size from 63 to 144 mm and non-reproductive clams ranged from 65 to 124 mm (Figure 6 A, B). At Clam Gulch, reproductive clams were 70 to 121 mm and non-reproductive clams were 71 to 125 mm (Figure 6 C, D). The frequency distribution of reproductive and non-reproductive clams at Ninilchik had two peaks while the distribution at Clam Gulch had a single peak. With regard to age, reproductive clams at Ninilchik were between 2 and 8 years old, while non-reproductive clams were between ages 2 and 7 (Figure 7 A, B). At Clam Gulch, clams were reproductive between ages 2 to 9, and non-reproductive clams were between ages 2 and 10 (Figure 7 C, D). As with the length distributions, age distribution at Ninilchik was bimodal, while it was unimodal at Clam Gulch.

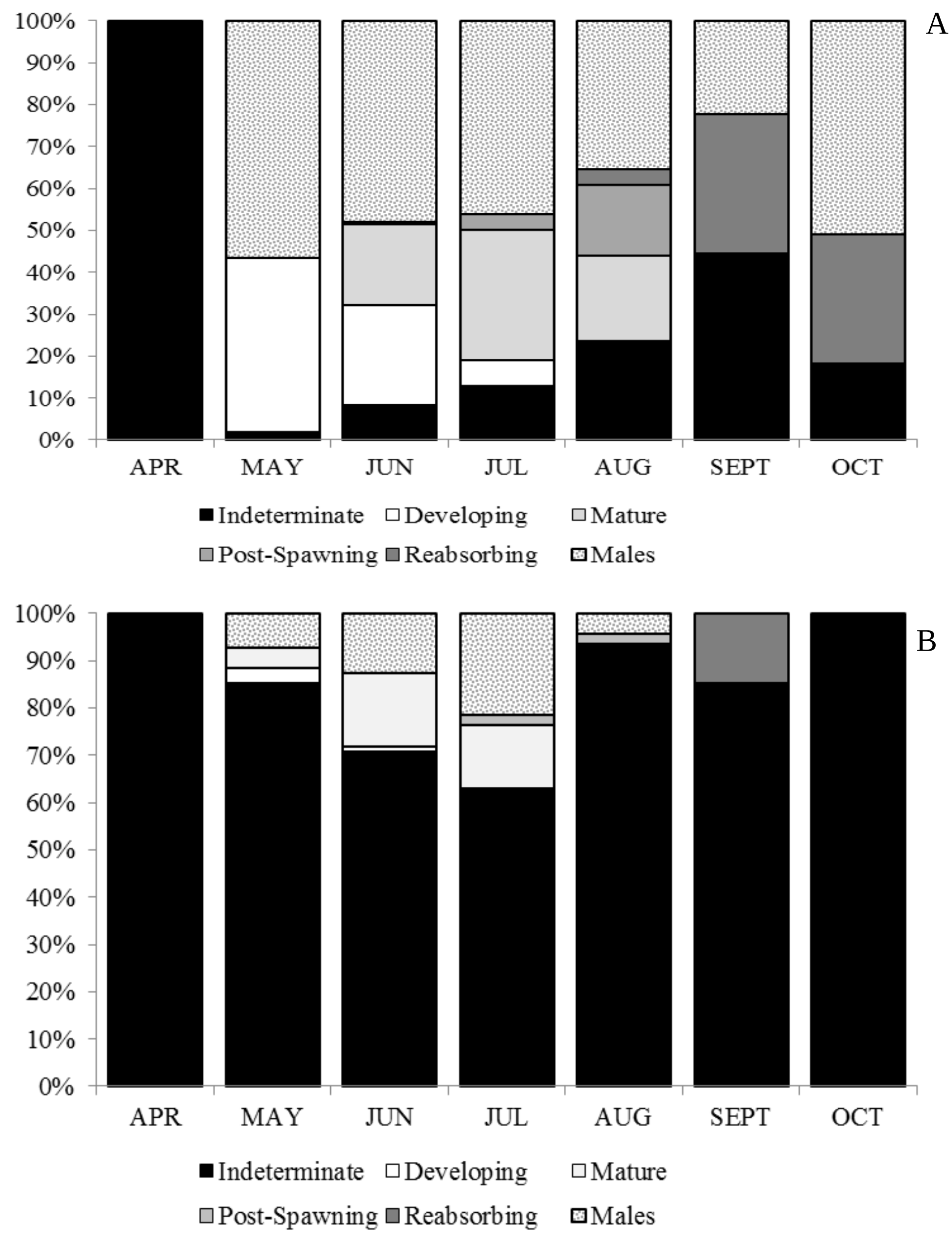

Figure 5. Frequency of reproductive stages of Pacific razor clams at Ninilchik (A) and Clam Gulch (B) in 2010, based on the female razor clam reproductive index described above.

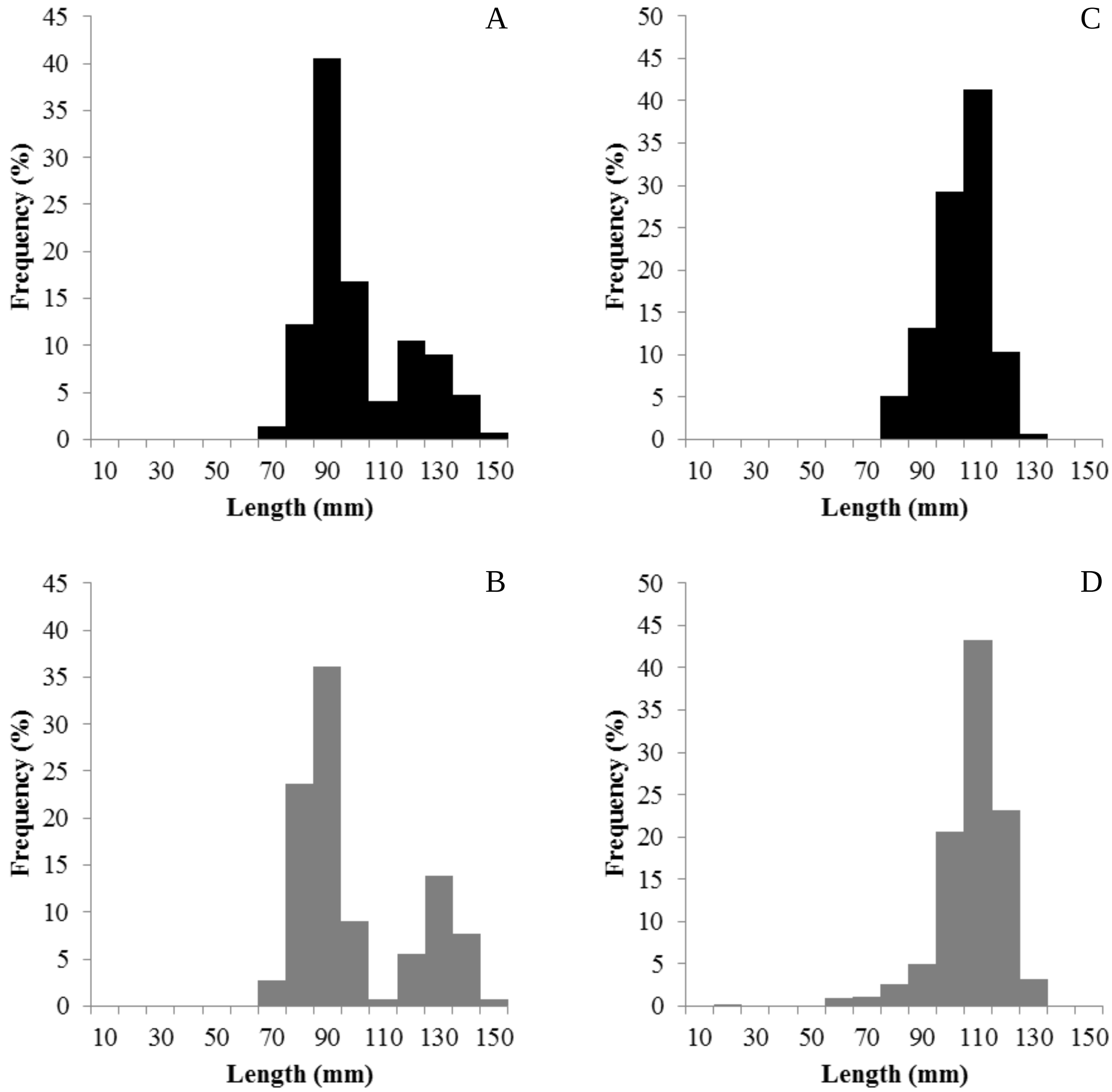

Figure 6. Length-frequency distribution of reproductive (top plots, black bars) and non-reproductive (bottom plots, grey bars) Pacific razor clams at Ninilchik (A, B) and Clam Gulch (C, D) in 2010. Both male and female clams are included in all graphs.

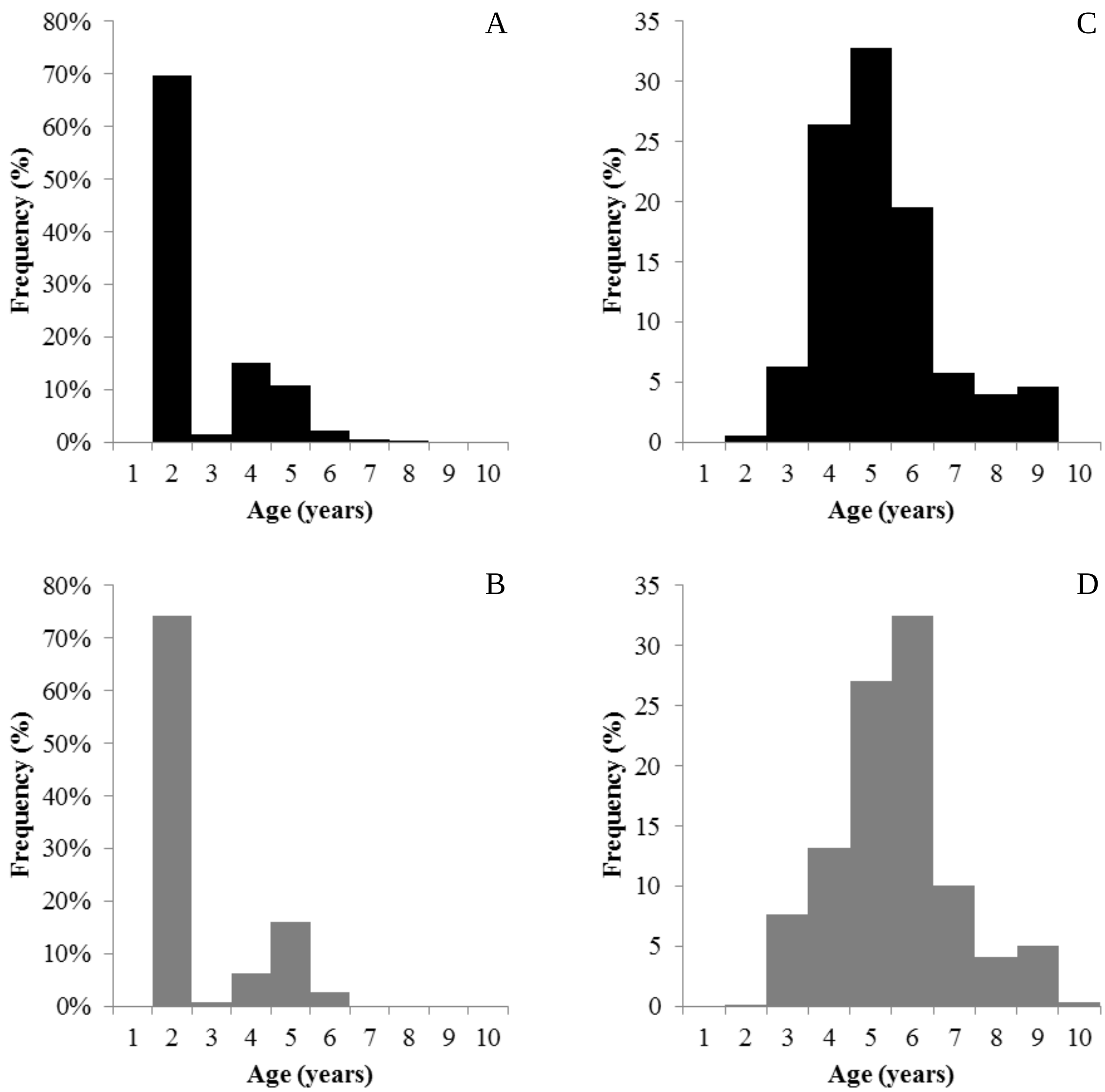

Figure 7. Age-frequency distribution of reproductive (top plots, black bars) and non-reproductive (bottom plots, grey bars) Pacific razor clams at Ninilchik (A, B) and Clam Gulch (C, D) in 2010. Both male and female clams are included in all graphs.

There were noticeable differences in reproductive status between razor clams collected at Ninilchik and Clam Gulch in 2010. At Ninilchik, 83% of all sampled clams (n=942) were reproductive, with approximately equal numbers of reproductive females (40%) and males (43%). The remaining 17% of clams were non-reproductive with indeterminate sex (Figure 8 A). At Clam Gulch, only 20% of all sampled clams (n=802) were reproductive, and these also had an even sex distribution (9% females and 11% males). However, the majority of clams (80%) were of indeterminate sex (Figure 8 B). It should be noted that the gonads of many clams at Clam Gulch were infested with an unidentified parasite (Figure 9), thus making determination of sex or reproductive status impossible. These clams were included in the indeterminate sex category.

The condition index of clams (dry tissue weight:shell weight ratio) at Clam Gulch was about 50% lower than for clams from Ninilchik at all sampling months during 2010 ($t_{(14)}$=6.467, p=<0.05; Figure 10 A). The condition index increased slightly in June at Ninilchik, but was relatively constant across months at Clam Gulch. Condition index was higher for razor clams at ages 2 and 3 and declined with increasing age at Ninilchik ($t_{(8)}$=8.767, $p<0.05$; Figure 10 B), while the condition index was relatively constant among all ages at Clam Gulch.

Length and age structure

The razor clam concentration at Ninilchik had a bimodal length-frequency distribution, with peak frequencies of 45 mm and 125 mm in 2009 and 85 mm and 120 mm in 2010 (Figure 11 A, B). The mean (± 1 standard deviation) length of all clams harvested at Ninilchik was 73 ± 44 mm in 2009 (n=690), and 91 ± 20 mm for 2010 (n=1073; Table 2). Razor clams sampled at Clam Gulch had a unimodal distribution (Figure 11 C, D). The mean length of all razor clams harvested at Clam Gulch was 104 ± 10 mm (n=361) in 2009 and 102 ± 12 mm (n=799; Table 3) in 2010. Overall, clams at Ninilchik had a significantly larger size at age than those harvested at Clam Gulch ($F_{(8, 2904)}$ = 5.953, p=0.0001; Figure 12), and the theoretical maximum length, based upon the von Bertalanffy growth equation, was larger at Ninilchik (147 mm) than at Clam Gulch (129 mm; Table 4). Likewise, in 2009 and 2010, growth performance measures of razor clams at Ninilchik were slightly higher (ϕ = 3.925, P = 6.096) than at Clam Gulch (ϕ = 3.626, P = 5.738; Table 4).

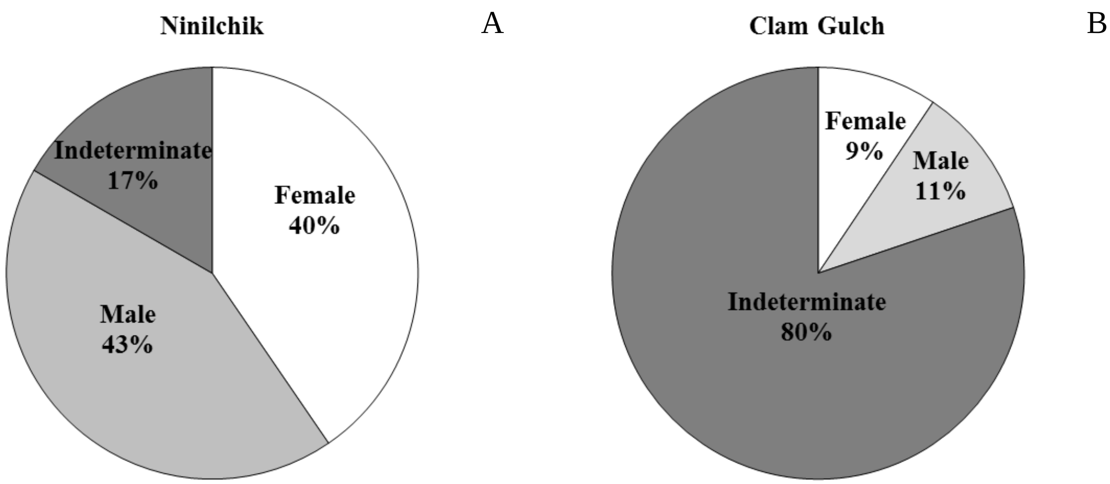

Figure 8. Percentage of reproductive and non-reproductive male and female Pacific razor clams at Ninilchik (A) and Clam Gulch (B) in 2010.

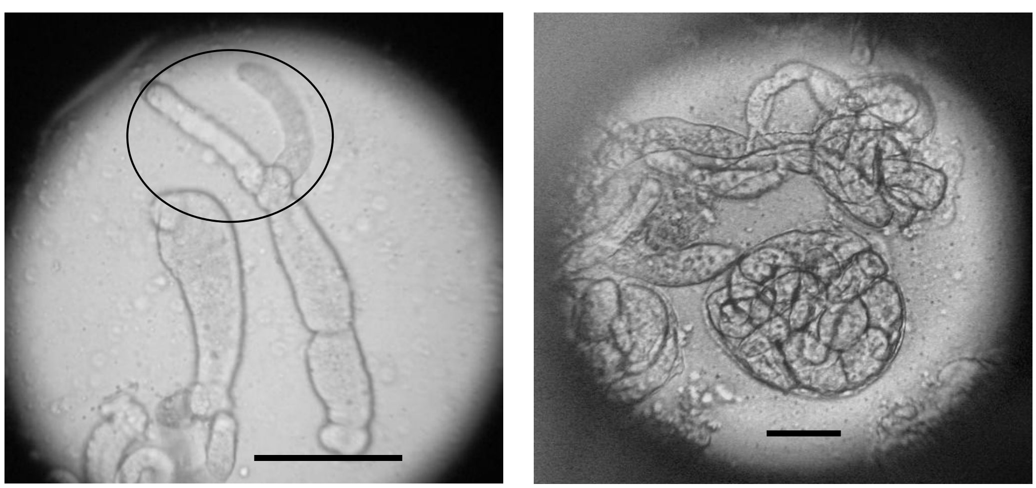

Figure 9. Unidentified parasite observed in gonad tissue of Pacific razor clams at Clam Gulch in 2010. Appendages referred to in text are indicated in the circle in the left photo (40-100x magnification). Scale bars are approximately 500 µm.

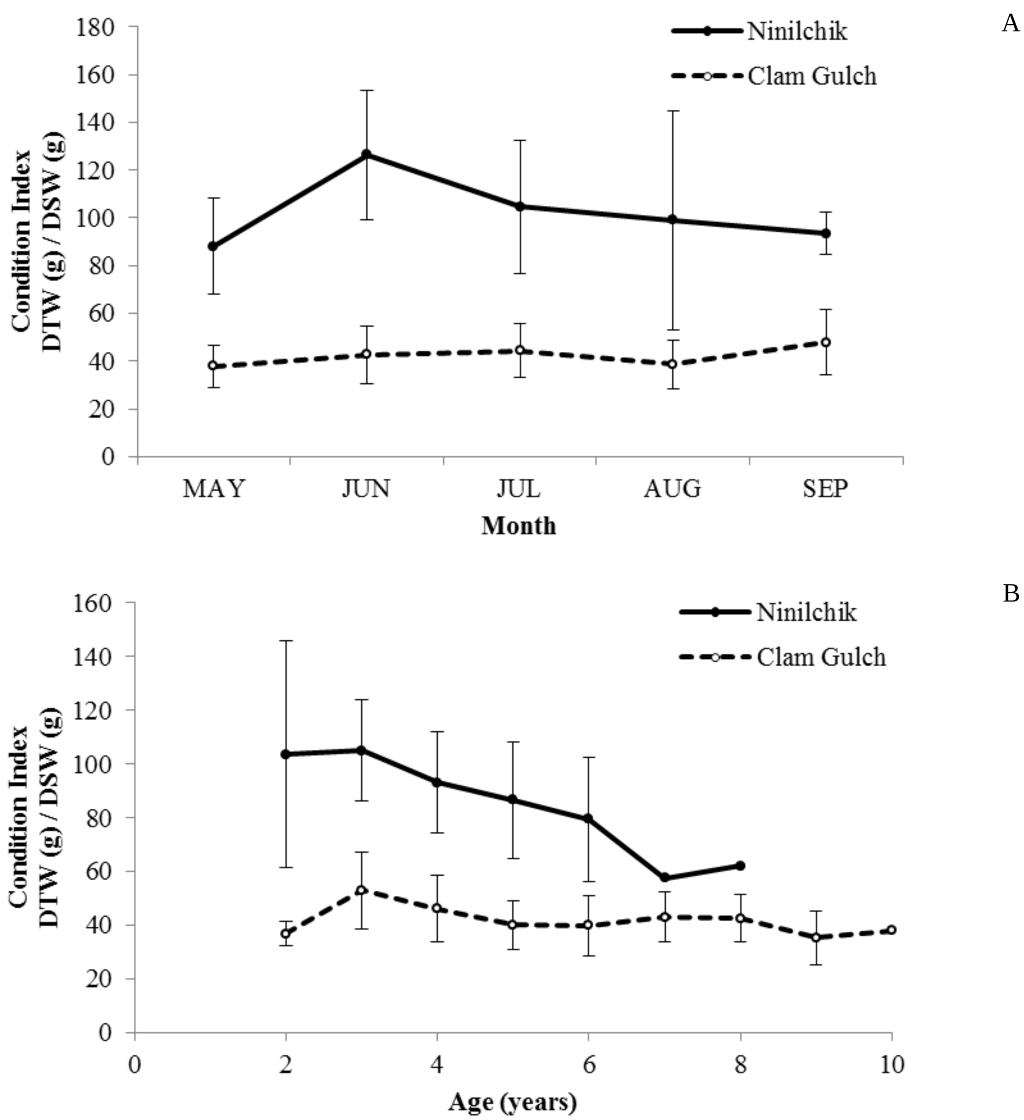

Figure 10. Mean condition index by month (A) and age (B) for Pacific razor clams at Ninilchik (solid lines) and Clam Gulch (dashed lines), May-September 2010. Error bars represent standard deviation.

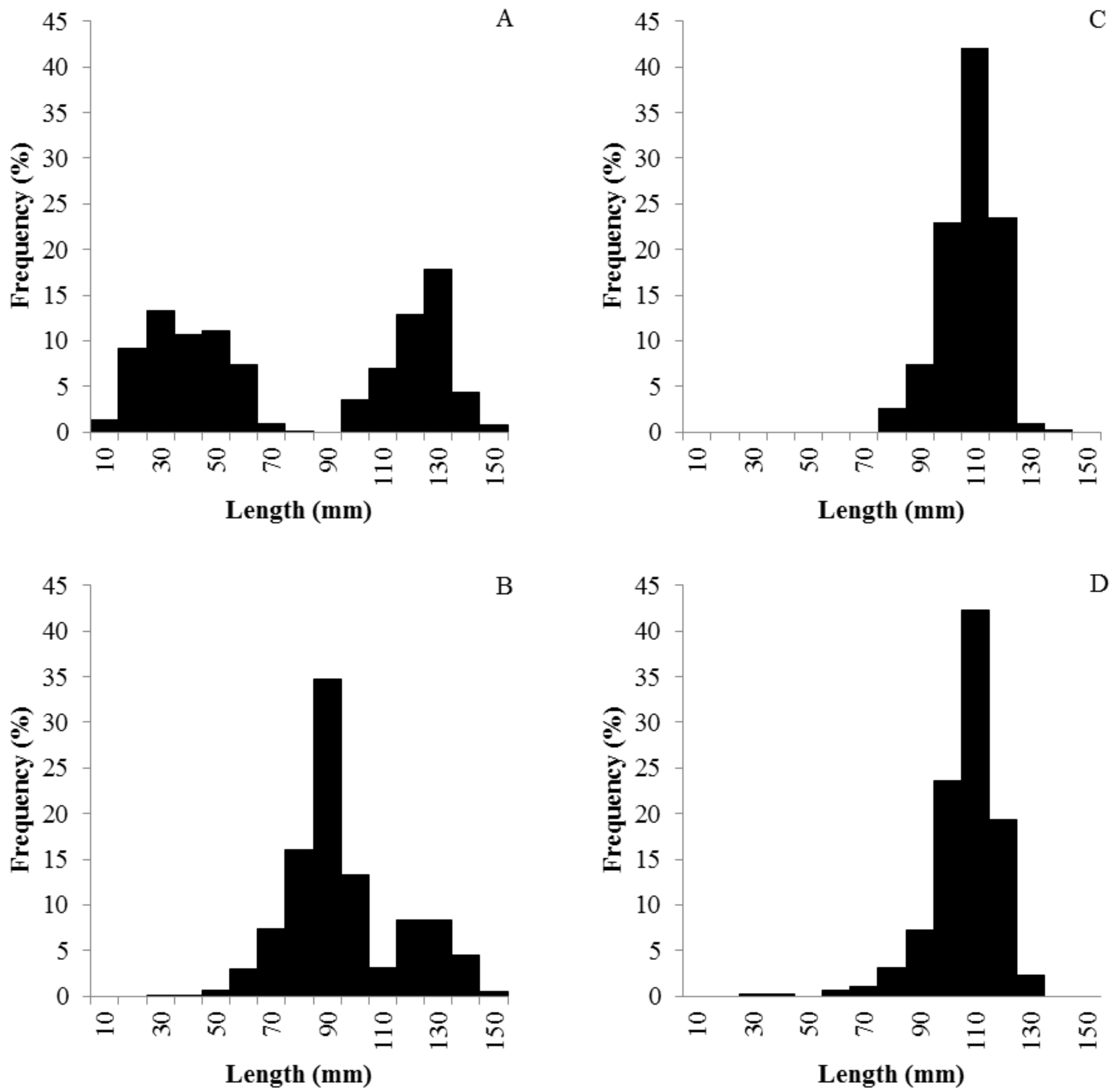

Figure 11. Length-frequency distribution of Pacific razor clams at Ninilchik in 2009 (A) and 2010 (B) and at Clam Gulch in 2009 (C) and 2010 (D).

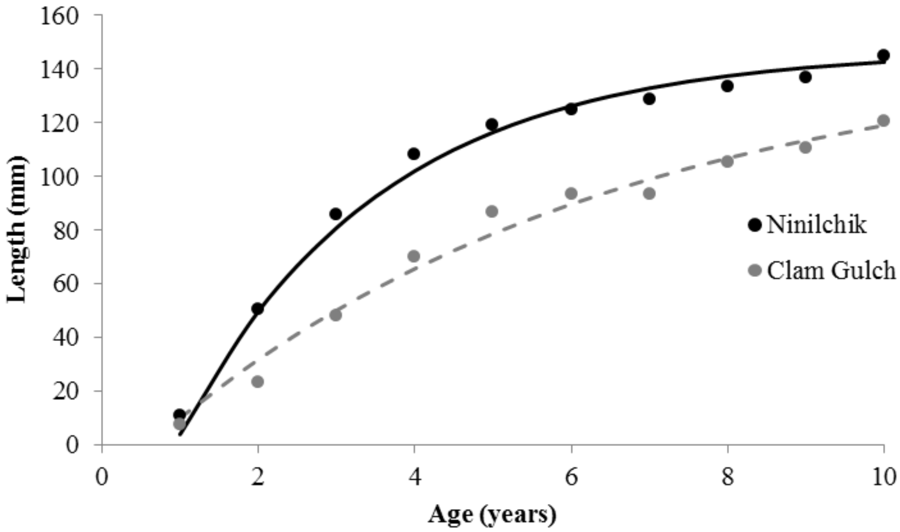

Figure 12. von Bertalanffy growth curves and mean length at age for Pacific razor clams from Ninilchik (solid line) and Clam Gulch (dashed line) during this study, 2009-2010.

The age-frequency distribution of razor clams at Ninilchik was bimodal in 2009; the largest number of individuals belonged to an age-1 cohort (hence, these clams were spawned in the fall of 2007 and are hereafter referred to as the 2007 age class), and a second cohort was composed primarily of older clams between 3-6 years of age (Figure 13 A). This same distribution was observed in 2010 when the 2007 age class reached age 2 and the older clams reached ages 4-7 years (Figure 13 B). The mean (± 1 SD) age of razor clams at Ninilchik during this study was 2.4 ± 1.6 years in 2009 and 2.7 ± 1.2 years in 2010 (Table 2). No distinct age cohorts could be distinguished at Clam Gulch in either study year (Figure 13 C, D). However, in 2009 there was a younger group consisting of ages 3 to 7 years and a separate peak at age-8 (Figure 13 C). The overall mean age of clams harvested at Clam Gulch during this study was 5.6 ± 1.6 years in 2009 and 5.5 ± 1.5 years in 2010 (Table 3). Overall, clams were significantly younger ($\chi^2_{(9)}$ = 1,618, $p < 0.05$) at Ninilchik than at Clam Gulch with 97% of the clams at Ninilchik at ages 1 to 5, and about half (52%) of the clams at Clam Gulch at ages 6 to 10 years.

Virtually no age 1 or 2 clams were detected at Clam Gulch, while 67% of clams collected at Ninilchik were age 1 or 2.

Historical length and age distributions

Historic length-frequency distributions based on ADF&G raw data from the Ninilchik area indicated that a greater number of larger clams occurred between 1994 and 2008 (110.3 ± 22.8 mm; Figure 14 A) relative to clams occurring during this study in 2009 and 2010 (83.9 ± 33.0 mm; Figure 14 C), $t_{(4651)} = 31.559$, $p < 0.001$). Mean clam length has declined by approximately 66% from 136 mm in 1994 to 91 mm in 2010 (Table 2).

There was a trend at Ninilchik towards fewer age classes and higher frequencies of younger age classes for razor clams in recent years (2009-2010; Table 2). The mean age at Ninilchik was age 4 ± 2 years from 1994 to 2008, and mean age during this study was age 3 ± 1 years (χ^2 (12) = 1555.390, $p < 0.05$; Figure 14 B, D). Data collected by the ADF&G in 2011, after this project was completed, showed that 96% of clams sampled in the Ninilchik area belonged to the 2007 age class (M.D. Booz, ADF&G, personal communication). Growth at Ninilchik has remained on the same growth trajectory since 1994, but with a decline in maximum age (age-10 in 2009-2010, compared with age-13 in the historical dataset; Figure 16 A).

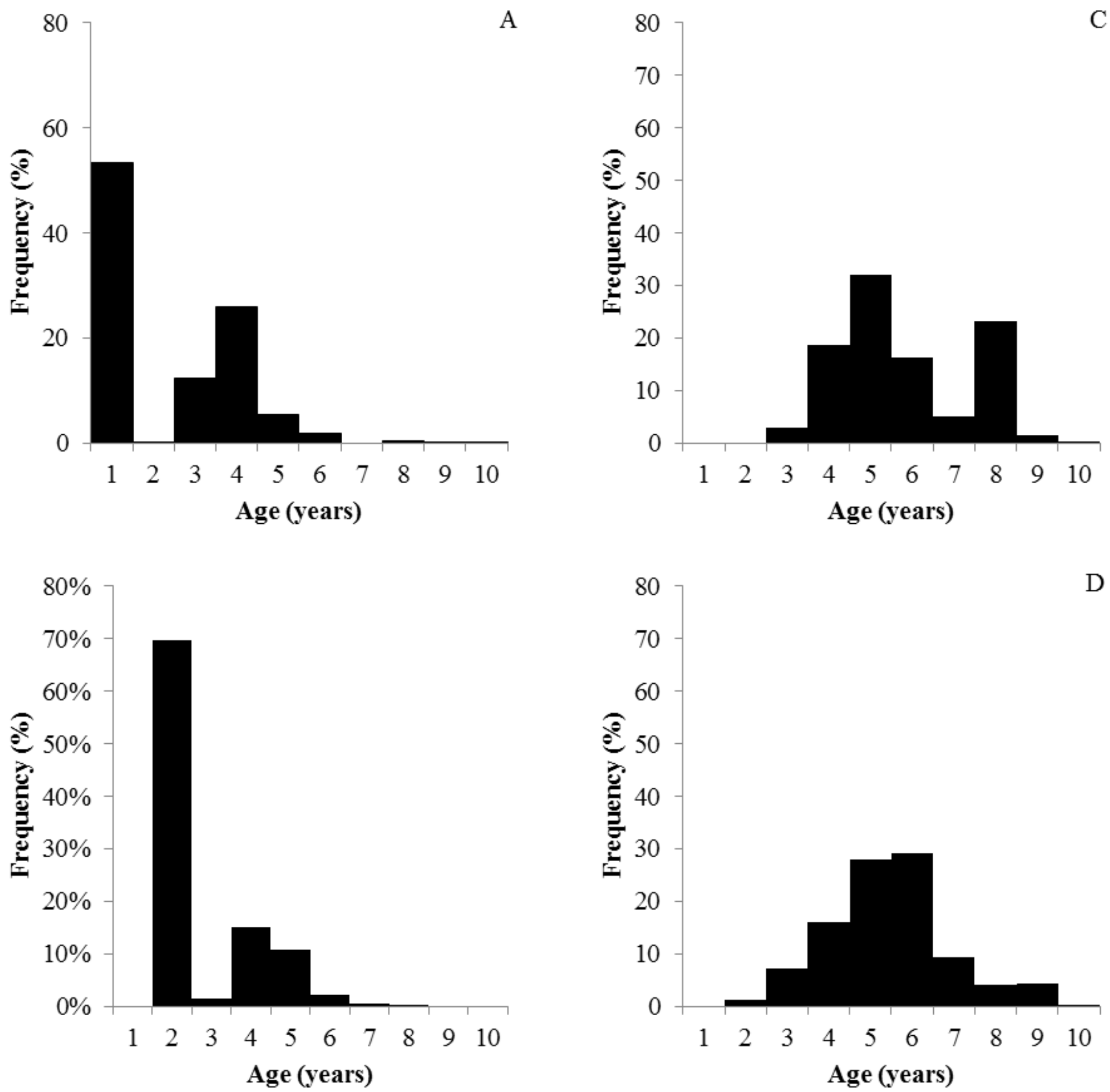

Figure 13. Age-frequency distribution of Pacific razor clams at Ninilchik in 2009 (A) and 2010 (B) and at Clam Gulch in 2009 (C) and 2010 (D).

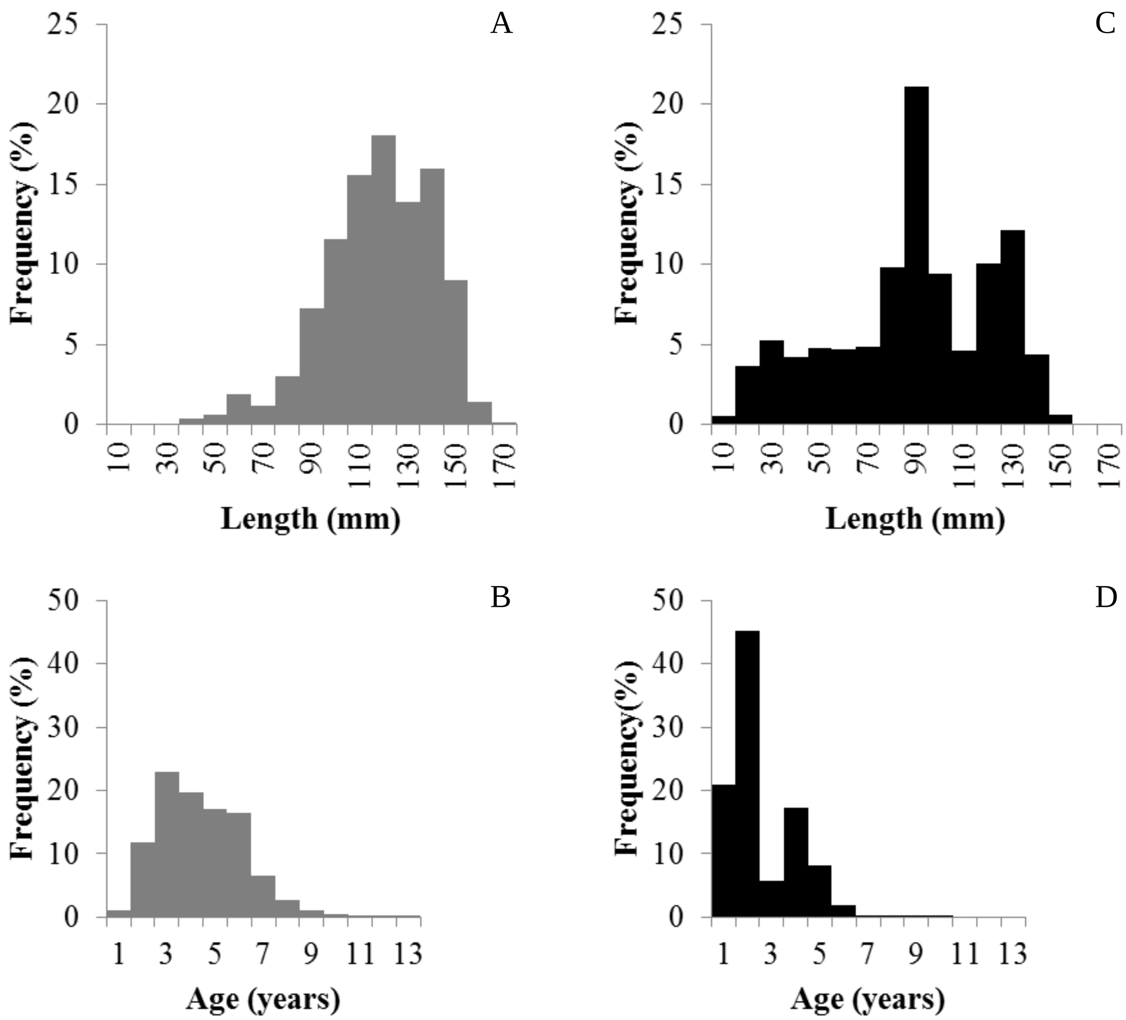

Figure 14. Historic length- (top plots) and age-frequency distributions (bottom plots) of Pacific razor clams at Ninilchik, 1994-2008 (A, B) and during this study, 2009-2010 (C, D).

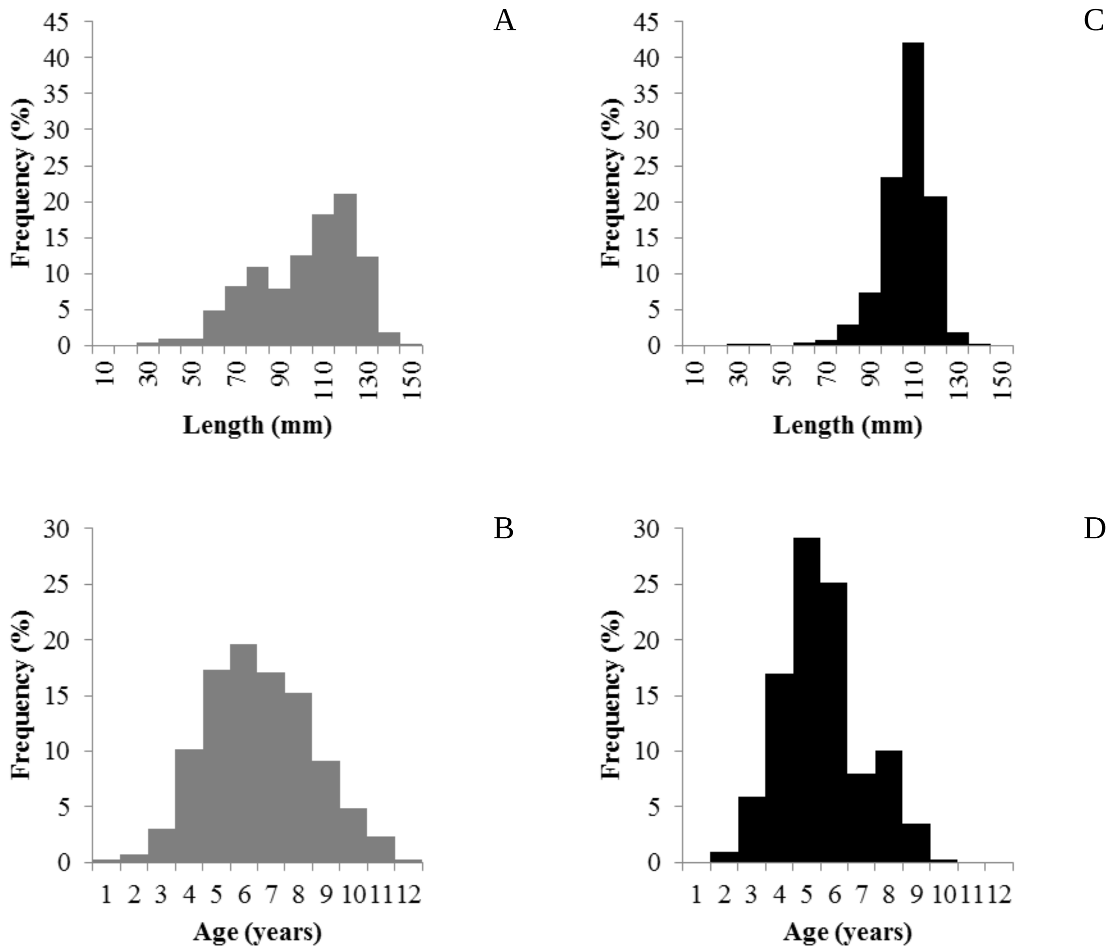

Figure 15. Historic length- (top plots) and age-frequency (bottom plots) distributions of Pacific razor clams at Clam Gulch, 2000-2008 (A, B) and during this study, 2009-2010 (C, D).

Table 2. Length and age characteristics of Pacific razor clams at Ninilchik, 1994-2010. The 1994-2008 data are from the ADF&G database (unpublished), 2009 and 2010 data (*) are from this study.

Year	n	Max Length (mm)	Min Length (mm)	Mean Length (mm)	SD of Length (mm)	Max Age (years)	Min Age (years)	Mean Age (years)	Median Age (years)	# of Age Classes Present
1994	219	162	102	136	11	12	3	6	6	10
1995	164	165	60	136	12	12	2	6	6	10
1996	170	166	74	127	19	10	2	5	5	8
1997	155	159	83	116	18	11	2	5	4	10
1998	161	156	55	111	21	8	2	4	4	7
1999	152	162	72	105	24	9	2	4	3	8
2000	148	145	77	116	14	9	2	4	3	8
2001	150	153	71	118	12	12	2	5	5	11
2002	147	146	31	109	31	10	1	4	5	10
2003	152	146	73	96	19	10	2	3	2	9
2004	150	149	40	108	19	13	2	4	3	11
2005	150	148	44	105	21	9	2	4	4	8
2006	149	140	54	108	16	8	2	5	5	7
2007	185	132	43	93	24	7	1	4	3	7
2008	161	140	71	107	13	7	2	4	3	6
*2009	873	150	6	73	44	10	1	2	4	9
*2010	1075	144	28	91	20	8	2	3	4	7

Table 3. Length and age characteristics of Pacific razor clams at Clam Gulch, 2000-2010. The 2000-2008 data are from the ADF&G database (unpublished), the 2009 and 2010 data (*) are from this study.

Year	n	Max Length (mm)	Min Length (mm)	Mean Length (mm)	SD of Length (mm)	Max Age (years)	Min Age (years)	Mean Age (years)	Median Age (years)	# of Age Classes Present
2000	140	140	59	115	12	12	2	8	8	11
2001	148	131	64	114	10	12	3	8	8	10
2002	146	133	90	115	9	11	1	8	8	9
2003	151	139	68	110	11	12	3	6	6	9
2004	149	132	75	109	10	11	4	7	7	8
2005	149	126	33	80	22	9	2	5	5	8
2006	150	114	23	73	19	11	2	5	5	10
2007	155	120	25	71	14	9	2	6	6	8
2008	154	110	55	88	12	10	2	6	7	9
*2009	387	131	73	104	10	10	3	6	6	8
*2010	818	126	25	102	12	10	2	5	5	9

Table 4 Values for von Bertalanffy growth constant (K), maximum length (L_∞), and growth performance indices (ϕ, P) for Pacific razor clams.

Species	K	L_∞ (mm)	ϕ	P	Location	Source
Pacific razor clam	0.590	144.22	4.09	6.25	Clatsop Beach, Oregon 45°48'7.89"N, 123°58'28.72"W	Hirschorn (1962)
	0.520	146.06	4.05	6.21	Clatsop Beach, Oregon 45°48'7.89"N, 123°58'28.72"W	Hirschorn (1962)
	0.384	147.11	3.93	6.10	Ninilchik, Cook Inlet, Alaska 60° 3'32.52"N, 151°39'31.65"W	Present study (2009-2010)
	0.254	129.17	3.63	5.74	Clam Gulch, Cook Inlet, Alaska 60°14'43.23"N, 151°23'51.71"W	Present study (2009-2010)

At Clam Gulch, there was a significant difference in the historical length-frequency distribution compared with the length-frequency distribution of the present study, ($\chi^2_{(15)}$ = 458.64, $p < 0.05$) (Figure 15 A, C). Likewise, there were significant differences in the age-frequency distribution between the historical dataset and the present study, (χ^2 (11) = 247.75, $p < 0.05$). The mean age at Clam Gulch between 2000 and 2008 was 7 ± 2 years, and between 2009 and 2010 was 6 ± 2 years (Figure 15 B, D). Clams appeared to grow faster during the 2009-2010 study until age-3, after which growth was slower than in 2000-2008. The maximum age of clams was also lower during this study (age-10) than in historic distributions (age-13; Figure 16 B).

Growth performance values calculated from historical ADF&G data for both locations indicated that clams at Ninilchik had consistently higher phi-prime (ϕ) values. The calculated overall growth performance value (P) was higher at Clam Gulch than Ninilchik in 2007, but lower in all other years (Figure 17). Both indices were statistically different between sites (ANOVA, $F = 143$ for ϕ, $F = 43$ for P; $p < 0.05$ both tests).

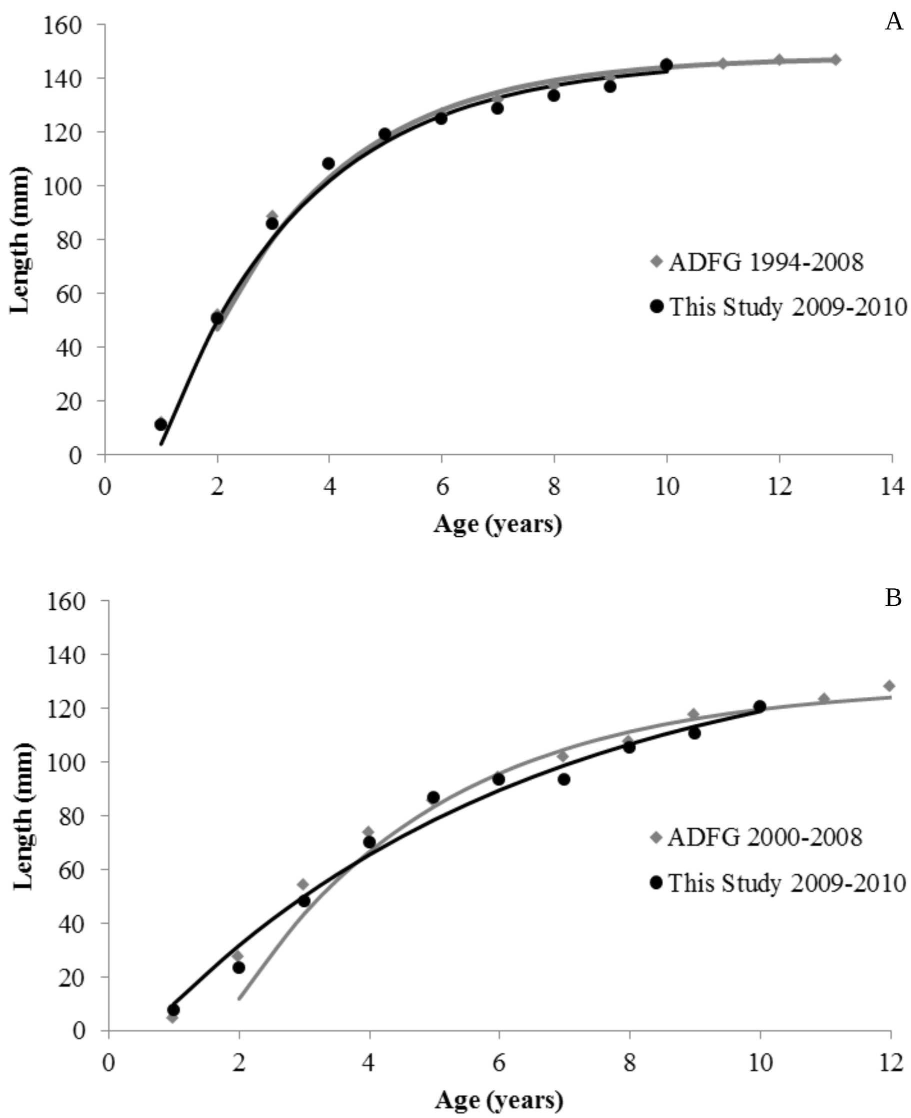

Figure 16. von Bertalanffy growth curves and mean length at age for Pacific razor clams sampled at Ninilchik (A) and Clam Gulch (B). Grey lines represent historic populations (ADF&G database), black lines represent this study (2009-2010).

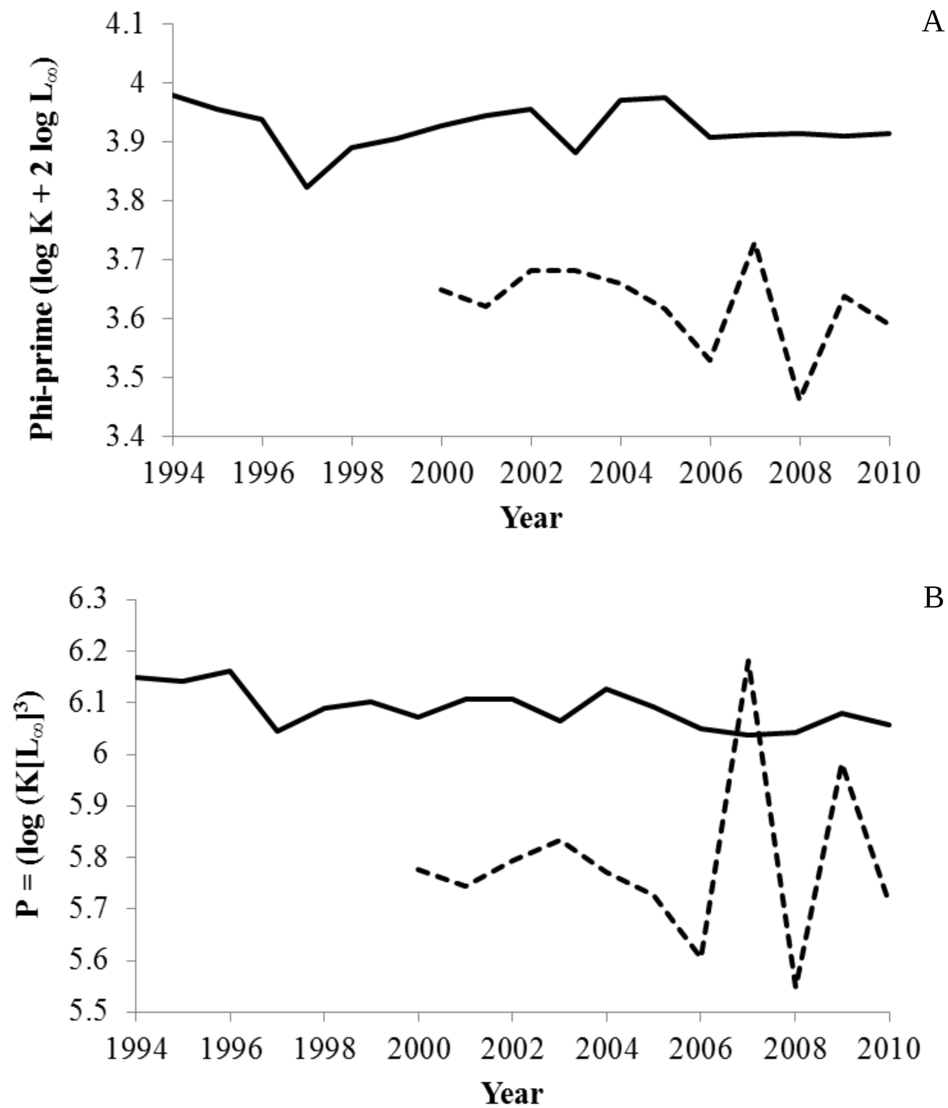

Figure 17. Historic growth-performance indices, phi-prime (A) and overall growth performance (B) at Ninilchik (solid lines) and Clam Gulch (dashed lines).

Detection of age-1 annulus

At the commencement of this study in June 2009, the 2007 age class at Ninilchik was entering its second growth season and had a distinct first annulus that was not preceded by a change in shell coloration, and no previous annuli were present. Clams from this brood grew approximately 9.8 mm per month in 2009 (Figure 18 A), with a mean length of 33.9 ± 14.2 mm. In 2010, this cohort (now the age-2 class) averaged 5.2 mm growth per month, and had a mean length of 85.3 ± 8.0 mm (Figure 18 B). During the second field season, the age-1 annulus was more difficult to detect in many clams from this 2007 cohort. In older clams, the first annulus was not distinctly detectable. Therefore, the first distinctly detectable annulus in eastern Cook Inlet razor clams is the age-2 annulus, which is consistent with current and historical aging methods employed by the ADF&G.

Environmental temperature monitoring

Mean monthly water temperatures (Figure 19 A) did not differ significantly between Ninilchik and Clam Gulch (ANOVA, $F = 1.0$; $p = 0.96$). Maximum mean water temperature was approximately 12°C at both sites during July and August and minimum water temperature was about -1°C in January and February. Likewise, sediment temperatures (Figure 19 B) were not significantly different between sites (ANOVA, $F = 2.3$, $p = 0.98$).

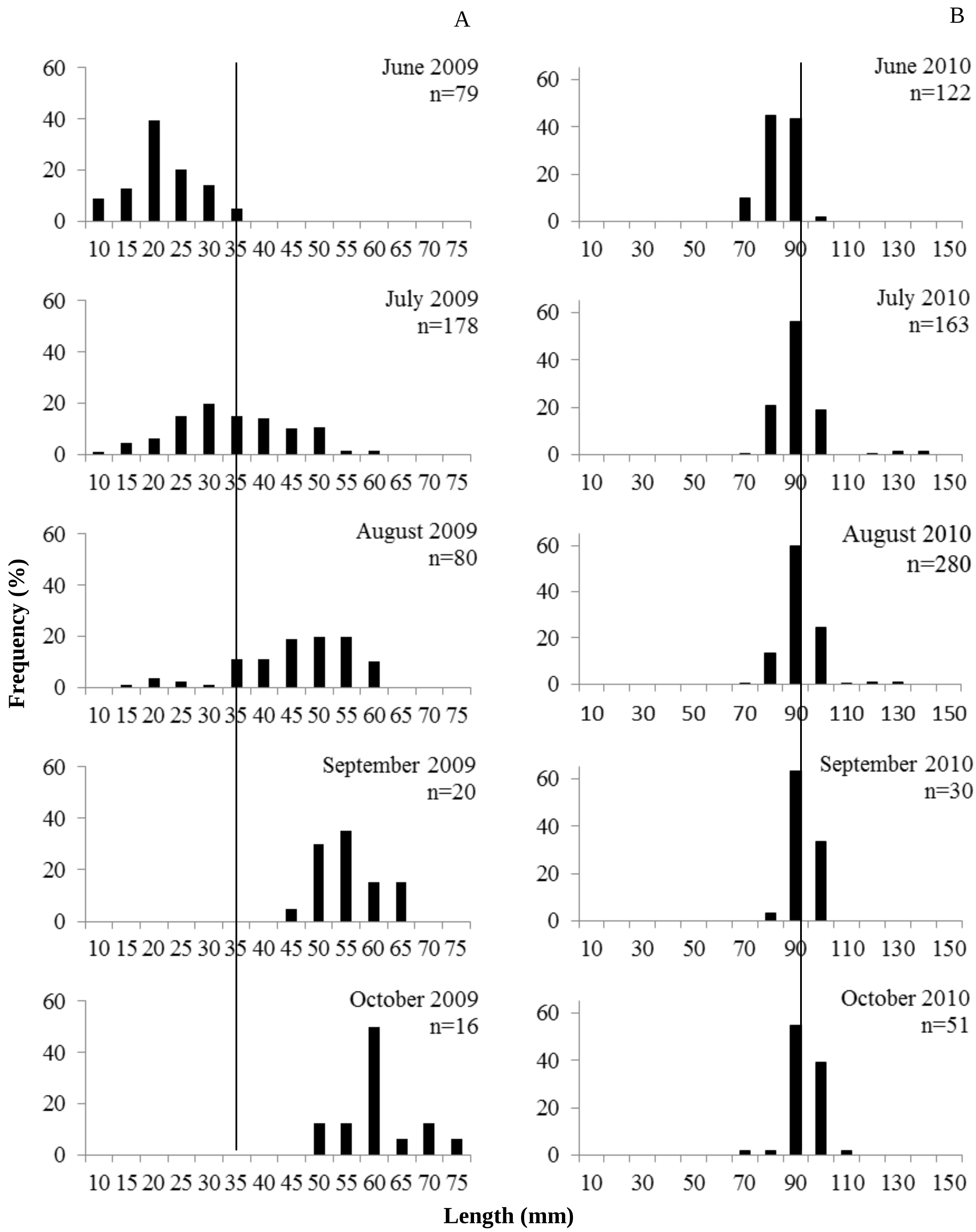

Figure 18. Length-frequency distributions of age-1 (June - October 2009) and age-2 (June - October 2010) Pacific razor clams collected at Ninilchik. The vertical lines mark the mean length of the 2007 brood in 2009 and 2010.

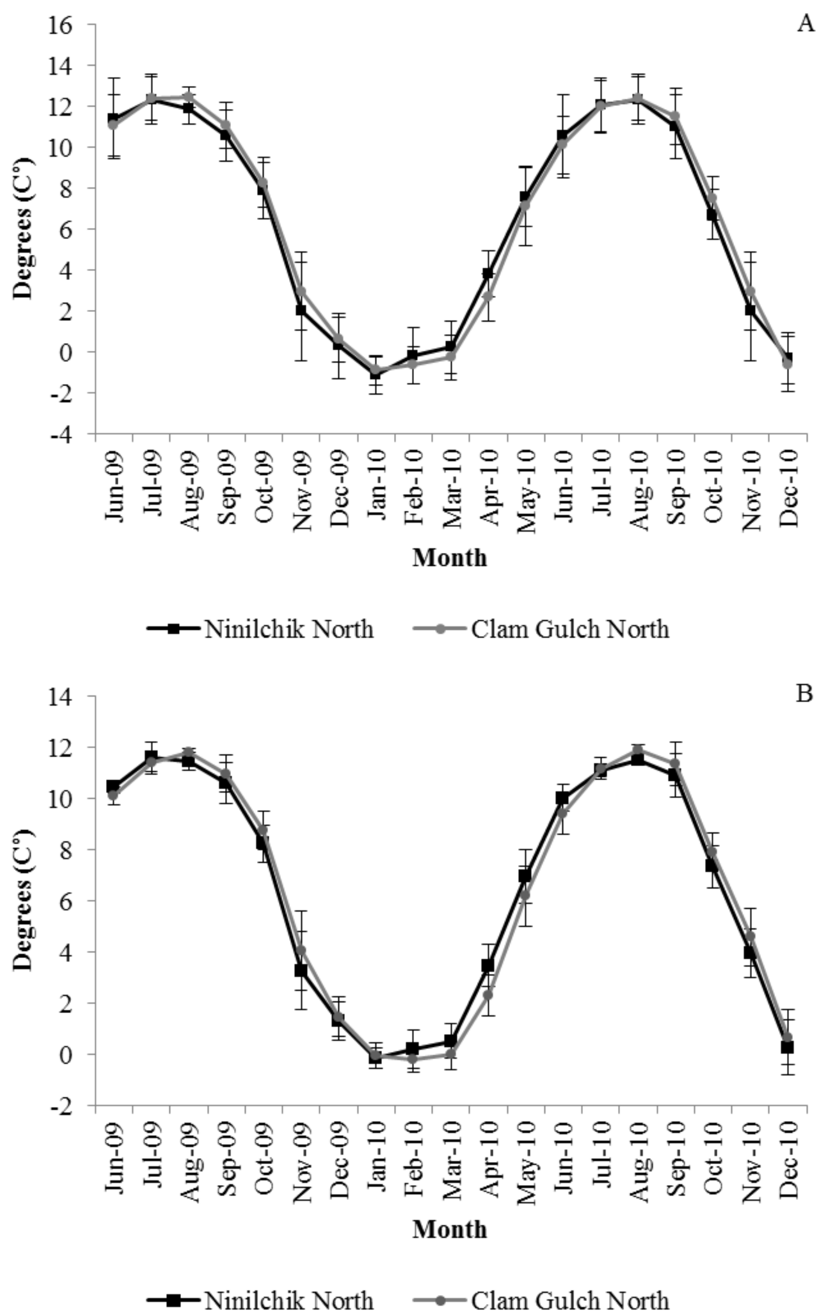

Figure 19. Mean monthly water temperatures (A) and substrate temperatures (B) at Ninilchik and Clam Gulch, June 2009 - December 2010. Temperatures did not differ significantly between sites ($p > 0.05$).

Discussion

Differences in reproductive output, growth rate, and age structure of Pacific razor clams were detected at two popular razor clamming beaches in eastern Cook Inlet, Alaska, located just 25 km apart. Additionally, there were distinct differences in the number of reproductive individuals detected at Ninilchik and Clam Gulch during the 2010 field season, and a weight-based morphometric condition index of clams from Clam Gulch was consistently lower than that of clams sampled at Ninilchik. Razor clams were found to mature at a smaller size and younger age than previously documented in eastern Cook Inlet (McMullen 1967). Analysis of historic ADF&G data since the mid-1990s to 2000s indicated that growth rates, as measured with the phi-prime and overall growth performance indices, have consistently been higher for clams at Ninilchik than for clams at Clam Gulch (ADF&G database, unpublished).

In invertebrate populations, reproduction and growth are closely linked and influenced by a number of environmental factors, most often seawater temperature and food availability (Bayne and Newell 1983, Brockington and Clarke 2001). Bivalves tend to grow faster at lower latitudes and slower at higher latitudes (Penttila and Dery 1988, Lassuy and Simons 1989, Brown et al. 2010). Latitude is a proxy for many physical-chemical controls, such as water temperature, nutrient availability, and photoperiod, which influence important biological processes, particularly seasonal primary production cycles (Harrison and Platt 1986). However, invertebrate growth may also vary on much smaller spatial scales, such as between or among sites, specific locations within the intertidal zone, or even among recruitment cohorts at the same location (Bourne and Quayle 1970, Quayle and Bourne 1972, Breese and Robinson 1981, del Piero and Dacaprile 1998). Some of this variation in clam reproduction and growth is likely to be driven by environmental factors influencing suspension feeding bivalves at a hierarchy of spatial scales

(Oresanz et al. 2000), such as local water characteristics, food availability (Richardson et al. 2004, Campbell et al. 2009), or differences in burrowing depth (de Goeji and Luttikhuizen 1998). The relationships between environmental factors, reproduction, and growth are not always clear, especially in borrowing species (Bricelj and Malouf 1984, Pilditch and Grant 1999), because it is very difficult to isolate the effects of various hydrographic features such as pH, salinity, turbidity, and dissolved oxygen (Seed 1980, Grant and Thorpe 1991, Ringwood and Keppler 2002).

Ninilchik and Clam Gulch are in relatively close proximity (25 km apart), but razor clam concentrations showed distinctly different length- and age-structures. Long-term water temperature loggers deployed by the National Oceanic and Atmospheric Administration (NOAA) at Seldovia, Alaska (lower Cook Inlet) indicate that water temperatures were generally warmer during winter 2010 (January to March) than in other years (http://cdmo.baruch.sc.edu/get/export.cfm). However, both water and sediment temperatures were measured in this study as important environmental variables influencing biological processes, but neither temperature measurement differed between the two study beaches. It is hence unlikely that seawater temperature was a driving force in the observed growth rate and maturity differences, or the longer spawning duration at Ninilchik. Similarly, temperature has been discounted as a driver of differential growth and reproduction of Manila clams (*Ruditapes decussatus*) in an estuary in Spain (Urrutia et al. 1999) as well as in blue mussels (*Mytilus edulis*) in California (Page and Hubbard 1987). In both cases, food availability was identified as the primary driver for population differences instead. Food availability for Pacific razor clams at the two beaches in eastern Cook Inlet was not assessed during this study. As filter feeders, razor clams depend on phytoplankton production and the quality and quantity of particulate organic matter (Holland and Dean 1977). Given the close proximity of the two beaches, overall primary production patterns are likely similar between sites, but future studies should investigate temporal and spatial availability and quality of particulate organic matter as food for razor clams at these two locations.

Recent changes in environmental variables in the Cook Inlet region have been linked to changes in the condition of several vertebrate and invertebrate species in the region. A reduction in the Cook Inlet beluga whale (*Delphinapterus leucas*) population has been attributed to environmental and climate change factors leading to reduced prey health, increased competition, and increased presence of killer whales (*Orcinus orca;* Carter and Nielson 2011). In addition, human influences such as fisheries management, water contamination, and anthropogenic-related noise likely play a role in the decrease of the beluga whale population (Carter and Nielsen 2011). During the same time period as the present study, a variety of diseases including tumors, parasites, and deformities were observed in Cook Inlet salmon (*Oncorhynchus* spp.), a primary prey item for beluga whales (Carter and Nielsen 2011). Cook Inlet fishermen reported decreased oil content in the fish and decreased sizes (Carter and Nielsen 2011). Additionally, the ADF&G has observed an increase in the number of small male Chinook salmon (*Oncorhynchus tshawytscha*), “jacks”, returning to Cook Inlet streams each year, and an overall reduction in Chinook salmon returns (ADF&G 2013). In a Cook Inlet shellfish study conducted in 2010, parasitic copepod, nematode, and gregarine (protozoan) infections were observed in shellfish collected at Seldovia, Nanwalek, and Port Graham in the lower Cook Inlet (Apeti et al. 2013). These authors found that although there were no human health concerns with regard to these parasites, there may be a potential for ecological effects, such as the fecundity, survival, and growth of their hosts (Johnson et al. 2004).

One factor that could have negatively affected growth and condition at Clam Gulch during this study may have been the parasitic infection that was observed in many clams in 2010. Parasitic infections often cause a decrease in growth rate and condition indices as parasites draw energy resources from the host organism (Hurd 1990, Smolowitz et al. 1998, Mercado-Silva 2005). Most commonly, energy to compensate for parasitic infections is diverted from reproductive processes, such as gonad development (Calvo-Ugarteburu and McQuaid 1998). In extreme cases, parasitic infections can lead to host sterilization (castration; Calvo-Ugarteburu and McQuaid 1998). In marine bivalves, such effects are most often caused by trematode parasites (Jonsson and André 1992, Calvo-Ugarteburu and McQuaid 1998, Valderrama et al. 2004). The mechanism of castration is not always clear, but may include mechanic effects (occupying gonadal area), cell lysis from parasite-released toxins, or disruptions of the endocrine control of gametogenesis (Coustau et al. 1993). Parasites observed in razor clams at Clam Gulch did not resemble trematodes as they appeared to have head appendages uncommon for flatworms (Brusca and Brusca 2003; see Figure 9). Spionid polychaetes would fit this morphological description, and they have also been found as parasites in clams, but their effects typically seem to focus on shell deformation (blistering) rather than effects on gonads (Riascos et al. 2008). Without additional information on the parasite identity and its life cycle, it remains unclear why only clams at Clam Gulch were infected and not those at Ninilchik.

Because the entire gonad region in Clam Gulch razor clams was occupied by parasites, these clams may have experienced castration; at a minimum, the reproductive output at this location was likely reduced. It is less clear if this parasite infestation affected growth, as found for other bivalve species with parasite infections (e.g., Taskinen 1998). Growth rates at Clam Gulch have historically always been lower than at Ninilchik, but populations have not been monitored for parasitic infections in the past. Thus, while the infection and the likely associated energetic cost may have caused some of the differences in reproductive patterns, growth rates, and condition indices between the two locations, it is unknown if this parasite infection is a recent event, or if it previously existed at Clam Gulch.

Growth indices (ϕ and P) of Pacific razor clams at Clam Gulch and Ninilchik were compared to those of other Pacific razor clam concentrations to assess how the high-latitude growth performance in Alaska compared with available data from lower-latitude locations (Table 6). Pacific razor clam concentrations in Oregon had higher growth rates and slightly higher growth index values relative to the eastern Cook Inlet clam concentrations. However, the maximum length of Oregon razor clams was similar to that of Ninilchik clams (Table 6). The Alaska location is the northern-most study site in this comparison, indicating that environmental conditions, such as lower water temperatures relative to southern latitudes, do not seem to limit overall growth performance.

The assessment of growth in bivalves depends on the accurate aging of the individuals, typically using the shell growth rings (Lassuy and Simons 1989). Age assessment, however, can be confounded by several factors including human error, environmental variation, and the presence of “false” annuli or check marks on the shells (Neves and Moyer 1988, Campbell et al. 2009). The disappearance of the first annulus in many individuals from the 2007 brood at Ninilchik as they grew older confirmed that the first visible annulus in older individuals is the age-2 annulus. This reaffirms the aging practices that have been employed by the ADF&G since the 1990s (ADF&G, unpublished). However, it was estimated in the 1970s and 1980s that clams in eastern Cook Inlet mature at approximately 100 mm, or age-3 at Ninilchik and age-4 at Clam Gulch (D. Nelson, ADF&G, unpublished data). In this study, some clams at Ninilchik and Clam

Gulch were already reproductive at age-2. Additionally, clams at Ninilchik were found be mature at sizes as small as 63 mm, and the smallest mature clam at Clam Gulch was 70 mm. These discrepancies with earlier data may either be due to differences in aging techniques (previous erroneous age assignment of the first visible annulus), or because clams have become reproductive earlier now than previously, possibly due to changes in environmental conditions such as salinity, turbidity, or food availability.

Differential larval dispersal and settlement at Ninilchik and Clam Gulch may also be a driver of the observed razor clam population differences. Evidence suggests that dispersal distances of some benthic marine organisms may be more demographically closed than previously thought (Cowen et al. 2000, Shanks 2009). Pelagic larvae can be retained in close proximity to their natal population (Cowen et al. 2000, Philippart et al. 2003), which would decrease the genetic mixing potential. Future research on the two razor clam beaches in eastern Cook Inlet should involve modeling of larval behavior and drift (e.g., André et al. 1993, Shanks et al. 2003, Harding et al. 2005, Shanks 2009), as well as genetic structure (e.g., Siegel et al. 2003), which could provide important information about source populations and variation in the age structure of adult clams. If beaches in East Cook Inlet are reseeded largely from their own area, it could explain low reproduction and recruitment in Clam Gulch and the decline in age classes present at Ninilchik compared with historical patterns. Self-seeding populations and the resulting low genetic diversity in razor clams at Clam Gulch could also enhance and explain the susceptibility to parasitic infection. However, the strong tidal current and the proximity of the two study beaches make it unlikely that the razor clam beaches in eastern Cook Inlet are entirely self-seeded. Understanding the spatial scales of their population connectivity is important for future management of this species.

Management considerations

Continued monitoring by the ADF&G after the present study was completed has confirmed the trends of declining razor clam populations observed here. In 2013, ADF&G estimated that the razor clam population in the Ninilchik area had declined to just 79,000 clams (ADF&G, unpublished). As a management response, the ADF&G issued an emergency order decreasing the daily harvest limits in eastern Cook Inlet from 60 clams to 25 clams per day (ADF&G Emergency Order No. 2-RCL-7-12-13). In addition to the decline in abundance, one age class made up approximately 96% of the clams at Ninilchik (ADF&G, unpublished data). Historically, 8 to 11 age classes have been present on that beach (see Table 2). Managers may have to consider closing the Ninilchik Beach to all razor clam harvesting until consistent annual recruitment is observed, and/or until the number of age classes present at Ninilchik is similar to historic razor clam distributions.

Currently, the ADF&G conducts periodic abundance surveys in eastern Cook Inlet. Between 2011 and 2013, the clam concentration at Ninilchik declined by an estimated 1.6 million clams. Prior to 2011, abundance estimates had not been made at Ninilchik since 2003. Continued annual surveys by the ADF&G would be useful to closely monitor razor clam abundance in eastern Cook Inlet; however, these surveys may be limited by budgetary constraints. The ADF&G also conducts annual age and length monitoring of nine study sites in eastern Cook Inlet. At each site, 150 clams are collected and staff spend an additional three weeks preparing, processing, and aging samples. Aerial and creel surveys indicate that approximately 80% of digger effort is focused at Ninilchik and Clam Gulch, while only 20% of the effort is focused in the other areas (Szarzi and Hansen 2009). The ADF&G may consider conducting less frequent abundance and age/length monitoring at beaches that receive less harvest pressure, such as Deep Creek, Whiskey Gulch, Setnet Access, and Cohoe. The time and costs saved would allow conducting annual surveys at the high-pressure harvest areas of Ninilchik and Clam Gulch. As another possible time-saving measure, the ADF&G could evaluate growth rates at all of its study sites in eastern Cook Inlet, and, where appropriate, consolidate nearby study sites and identify a single index site in each area where future abundance and exploitation data would be collected.

In addition to abundance surveys, the ADF&G may consider implementing regular monitoring for parasites in eastern Cook Inlet to determine whether the parasites observed at Clam Gulch in 2010 are still present at that beach, and whether they occur in other locations. It would also be useful to have the parasite identified, so that biological and human health consequences can be assessed.

This study determined that Pacific razor clams are harvestable at smaller sizes (approximately ≥ 50 mm) than the size currently identified by the ADF&G (≥ 80 mm). Because current regulations stipulate that diggers must keep the first 25 clams dug, regardless of size, the ADF&G should consider reevaluating and, if appropriate, updating its classification of exploitable clams, which may impact future ADF&G harvest estimates.

Conclusions

This study presented comprehensive data on aging, growth, spawning, and reproduction for the two most popular razor clam beaches located within the eastern Cook Inlet fishery. The information that was obtained during this study has already begun to contribute to the ADF&G's management of razor clams in this region. Most notably, new knowledge was gained that razor clams in eastern Cook Inlet are maturing at a smaller length and younger age than previously documented in Alaska. This is also the first Pacific razor clam study in eastern Cook Inlet that evaluated spawn-timing, and it was established that razor clams produce a show and are exploitable at a much smaller size than previously thought. Using existing historic and new data, it was determined that there is a marked difference in growth rates, age distribution, and morphometric condition indices at Ninilchik and Clam Gulch. As managers of the eastern Cook Inlet fishery respond to changes in this population, the data provided by this study will be critical for developing ways to sustainably manage and protect razor clams in this region.

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